Silvicultural Options to Promote Resilience of Northern Great Lakes *Fraxinus nigra* (Black Ash) Forests following Emerald Ash Borer (*Agrilus planipennis*) Invasion

A Dissertation
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

Christopher Edward Looney

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Anthony D'Amato, Ph.D., Adviser

May 2017

Acknowledgements

I am immensely grateful to my adviser, Dr. Anthony D'Amato, for being an outstanding mentor. I owe my degree in large part to his knowledge, enthusiasm, and unwavering support. Very special thanks to my committee members, Brian Palik of the USDA Forest Service Northern Research Station, Shawn Fraver of the University of Maine School of Forest Resources, and Lee Frelich of the University of Minnesota Department of Forest Resources, for generously sharing their expertise, advice, and constructive comments. Thanks also to Robert Slesak of the Minnesota Forest Resources Council for contributing to the hydrological aspects of this research. As co-authors of the articles that form the core of this dissertation, I appreciate the many hours each of you invested in reviewing successive drafts and making substantive and editorial suggestions.

Funding for this dissertation was provided by the Minnesota Environment and Natural Resources Trust Fund to the Legislative Citizens Committee on Minnesota Resources, the USDA Forest Service Northern Research Station, and the US Department of Interior Northeast Climate Center. I am grateful to the Department of Forest Resources of the University of Minnesota for the Frederick and Philip Noel Knorr and Northwest Paper Foundation Fellowships, which helped support my studies, as well as to the University of Minnesota Graduate School for awarding me a Doctoral Dissertation Fellowship.

Thanks to Gary Swanson of the Chippewa National Forest for initially suggesting this project and to the Chippewa National Forest staff who provided logistical support. Doug Kastendick of the USDA Forest Service Northern Research Station planned harvest

treatments and, along with Mike Reinikainen, Kyle Gill, and Nick Jensen of the University of Minnesota, assisted with tree planting. Very special thanks to Mitchell Slater of the Northern Research Station for coordinating tree planting, maintaining measurement subplots, and serving as a co-author on the understory vegetation article. This research could not have been completed without the many field assistants: Laura Broadhead, Vi Bui, Lucas Dykstra, Isabel Harger, Tom Hefferman, Ian Hetterich, Ellie McCann, Jamie Peeler, Andrew Rothrock, Madeline Sarcone, and Glenn Skiles.

I am grateful to NRC Research Press and Elsevier for allowing me to republish the following journal articles as dissertation chapters and to the anonymous reviewers who offered constructive suggestions:

- Chapter 3: Reprinted from the Canadian Journal of Forest Research, Vol. 45, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer-threatened *Fraxinus nigra* forests in Minnesota, USA, pp. 1728-1738, © 2015 Christopher E. Looney, Anthony W. D'Amato, Brian J. Palik, Robert A. Slesak, with permission from NRC Research Press. http://dx.doi.org/ 10.1139/cjfr-2015-0129;
- Chapter 4: Reprinted from Canadian Journal of Forest Research, Vol. 47, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer-threatened *Fraxinus nigra* forests in Minnesota, USA, pp. 183-192, © 2016 Christopher E. Looney, Anthony W. D'Amato, Brian J. Palik, Robert A. Slesak, with permission from NRC Research Press. http://dx.doi.org/ 10.1139/cjfr-2016-0369;

- Chapter 5: Reprinted from Forest Ecology and Management, Vol. 389, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Slater M.A., The response of *Fraxinus nigra* forest ground-layer vegetation to emerald ash borer and management strategies in Minnesota, USA, pp. 352-363, © 2017 with permission from Elsevier. http://dx.doi.org/10.1016/j.foreco.2016.12.028.

Finally, I offer my heartfelt thanks to my parents and to the many friends who supported me on this journey. I couldn't have done it without you.

Abstract

Fraxinus nigra (black ash), a dominant species of northeastern North American wetland forests, is threatened by the invasive insect, emerald ash borer (*Agrilus planipennis,* EAB). The potential for one or more tree species to replace *F. nigra* and approaches for facilitating this replacement have not been explored. To fill these knowledge gaps, this research examined: (1) the influence of competition and climate on the growth of mature *F. nigra* in association with *Tilia americana (*basswood), *Populus tremuloides* (quaking aspen), and *Thuja occidentalis* (northern white-cedar) at the mesic, moist, and wet *F. nigra* forest margins, respectively; (2) the survival and growth of planted seedlings of 12 potential *F. nigra* replacement species under four canopy treatments: unharvested control, clearcut, *Fraxinus* girdling to emulate EAB, and group selection; and (3) the response of *F. nigra* forest groundlayer plant communities to treatment-induced canopy changes. The research goals were to determine (1) how the influences of climate and competition vary by species in *F. nigra* forests and whether these factors shift in importance along a gradient of waterlogging stress; (2) the most promising combinations of species and treatment for silvicultural efforts to maintain post-EAB forest function; and (3) the extent to which natural regeneration of associated tree species can be expected to aid in maintaining post-EAB forest cover, as well as the potential effects on this regeneration of EAB- and treatment-induced shifts in groundlayer community composition. The main findings were that mature *F. nigra* had slower growth and appeared more sensitive to competition than *T. americana* and *P. tremuloides*, while having similar growth and appearing less sensitive to competition than *T. occidentalis*. *Fraxinus nigra* growth

showed greater sensitivity to precipitation and temperature across the gradient of waterlogging stress relative to the three associated species. Canopy treatment type interacted with species to influence the survival and relative growth rate (RGR) of planted seedlings. Planted seedlings of shade-intolerant species generally had moderate-to-low survival and high RGR across treatments, while shade-tolerant species had higher survival with lower RGR. Natural tree regeneration varied by treatment and fell short of *F. nigra* forest stocking recommendations. Graminoid cover increased in the clearcut treatment, while bottomland shrubs and wetland indicator species were more numerous in the control and girdle. Overall, the findings suggest that planting seedlings of non-*Fraxinus* tree species with or without overstory treatment as EAB approaches is a potentially viable and necessary management option for sustaining ecosystem services in *F. nigra* wetlands. Site, species, and canopy treatment selection should be coordinated to maximize artificial regeneration success.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

Fraxinus nigra Marsh. (black ash) wetland forests in northeastern North America are threatened by the introduced Asian insect, emerald ash borer (*Agrilus planipennis* Fairmaire, EAB), which causes lethal girdling damage to all North American *Fraxinus* spp. (Pugh et al., 2011). In southern Michigan mixed-*Fraxinus* forests near the invasion epicenter, EAB has resulted in greater than 97% mortality in *Fraxinus* spp. trees with a diameter at breast height (DBH) ≥ 2.5 cm (1 in, Herms and McCullough, 2014), with few or no newly germinated *Fraxinus* seedlings observed on heavily infested sites (Klooster et al. 2014). In *F. nigra* wetland forests, studies suggest hydrological changes associated with the loss of the *F. nigra* overstory may also lower regeneration of already sparse non-*Fraxinus* tree species (Palik et al., 2012; Slesak et al., 2014). As a result, the continued spread of EAB could potentially cause widespread loss of overstory cover and ecosystem function in the wetland forest systems where *F. nigra* is presently dominant (Iverson et al. 2016).

A possible management option is promoting increased regeneration of non-*Fraxinus* tree species, such as *Populus balsamifera* L. (balsam poplar), *Larix laricina* (Du Roi) K. Koch (tamarack), *Acer rubrum* L. (red maple), and *Ulmus americana* L. (American elm; Slesak et al., 2014). The potential for one or more tree species to replace *F. nigra* and approaches for facilitating this replacement have not been adequately explored. To fill this research gap, this dissertation explores pre-invasion *F. nigra* forest ecology and silvicultural strategies, to inform efforts to manage the effects of EAB in *F.*

nigra wetlands.

Understanding pre-invasion forest ecology is critical to the design of effective strategies to restore or sustain forests threatened by invasive insects or pathogens (Waring and O'Hara, 2005). However, relatively little is known about the growth response of *F. nigra* and associated tree species to tree competition, climate, and waterlogging stress at the topographic *F. nigra* forest margins (Dudek et al., 1998). In the two prior studies of competition in *F. nigra* forests, Benedict and Frelich (2008) found tree competition exerted little influence on *F. nigra* growth at either upland or lowland sites, whereas Looney et al. (2016) found competition limited *F. nigra* growth, with the effect weaker on wetter lowland sites. Previous studies that examined the influence of climate in *F. nigra* forests found *F. nigra* sensitivity to spring precipitation appeared to increase with site flooding (Tardif and Bergeron, 1993), and *F. nigra* growth at a drier, upland site showed temperature sensitivity suggestive of summer drought stress. In contrast, growth of the bottomland conifer, *Thuja occidentalis* L. (northern white-cedar) appeared sensitive to summer drought on both floodplain and upland sites (Tardif and Bergeron, 1997), suggesting growth-climate relationships may differ between *F. nigra* and associated species. Chapter 2 extends these lines of research to examine the influence of competition and climate on the growth of *F. nigra* in association with *Tilia americana* (basswood) at two mesic sites, *Populus tremuloides* (quaking aspen) at two moist sites, and *T. occidentalis* at two wet sites. Its goals are to ascertain how the effects of competition and climate vary by species and whether the importance of these factors shifts with changing abiotic stresses across a gradient of waterlogging stress in *F. nigra* wetland forests.

Forest management strategies such as artificial regeneration and overstory treatments have been suggested to restore forests impacted by introduced disturbance agents (Waring and O'Hara, 2005). For example, group selection treatments can be used to adjust the amount of light that reaches the forest floor, as well as to ameliorate microclimate effects and changes in site hydrology, thus enhancing regeneration success (Slesak et al., 2014; Smith et al., 1996). Artificial regeneration and group selection treatments increased recruitment of associated tree species in *Salix nigra* Marshall (black willow) wetland forests, with species selection exerting a greater influence than the size of the canopy opening (Dulohery et al., 2000). No prior studies have examined the use of artificial regeneration and overstory treatments in *F. nigra* forests. Using an operational field scale experiment, Chapter 3 examines the survival response and Chapter 4 the growth response of planted seedlings of potential *F. nigra* replacement tree species under four canopy treatments: uncut forest (control); girdling of all *Fraxinus* spp. trees ≥ 6 cm DBH to emulate EAB-induced mortality; group selection; and unharvested control. Based on the results of the two chapters, the most promising combinations of replacement species and overstory treatment are identified to aid in the development of strategies to manage the effects of EAB in *F. nigra* forests.

Alterations to the forest canopy may have a profound impact not only on the growth of planted seedlings, but on natural tree regeneration and the size and composition of ground-layer plant communities (Hausman et al., 2010). An observational study of clearcutting effects in *F. nigra* forests suggests pre-invasion logging and the loss of *F. nigra* to EAB would raise water tables, shift the structure and composition of the

herbaceous understory, and impede tree regeneration (Erdmann et al., 1987). Both pre-invasion logging and EAB-induced mortality greatly increased herbaceous cover in southern Michigan forests with a small component of *Fraxinus* spp., although pre-invasion logging was associated with more drastic environmental changes that included an increase in the number of invasive plant species (Hausman et al., 2010). No scientific research to date has examined the effects of canopy treatments on *F. nigra* forest ground-layer vegetation. Chapter 5 takes advantage of the treatment plots established for the planting experiment to investigate the effects of EAB and overstory treatment on established tree regeneration, as well as the size and composition of the *F. nigra* forest shrub and herbaceous layers. Its aims are to determine to what extent established regeneration of associated tree species is likely to contribute to the maintenance of forest cover, assuming the practical loss of *F. nigra*, and whether overstory management would aid or hinder this regeneration.

Chapter 6 summarizes and synthesizes the results of the four data chapters. It begins by reviewing the main findings, elaborates on the management implications discussed in previous chapters, and concludes with suggestions for potential areas of future research.

References

Benedict, M.A., Frelich, L.E., 2008. Site factors affecting black ash ring growth in northern Minnesota. For. Ecol. Manag. 255, 3489–3493. http://dx.doi.org/10.1016/j.foreco.2008.02.029.

Dudek, D.M., McClenahen, J.R., Mitsch, W.J., 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. Am. Midl. Nat. 140, 233–244. http://dx.doi.org/10.1674/0003-0031(1998)140[0233:TGROPD]2.0.CO;2.

Dulohery, C.J., Kolka, R.K., McKevlin, M.R., 2000. Effects of a willow overstory on planted seedlings in a bottomland restoration. Ecol. Eng. 15, S57–S56. http://dx.doi.org/10.1016/S0925-8574(99)00072-5.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115.

Hausman, C.E., Jaeger, J.F., Rocha, O.J., 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. Biol. Invasions 12, 2013–2023. http://dx.doi.org/10.1007/s10530-009-9604-3.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts and management. Annu. Rev. Entomol. 59, 13–30. http://dx.doi.org/10.1146/annurev-ento-011613-162051.

Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx/doi.org/10.1007/s10021-015-9929-y.

Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 16, 859–873. http://dx.doi.org/10.1007/s10530-013-0543-7.

Looney, C.E., D'Amato, A.W., Fraver, S., Palik, B.J., Reinikainen, M.R., 2016. Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. For. Ecol. Manag. 375, 238–248. http://dx.doi.org/10.1016/j.foreco.2016.05.050.

Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. For. Ecol. Manag. 269, 26–30. http://dx.doi.org/10.1016/j.foreco.2011.12.020.

Pugh, S.A., Liebhold, A.M., Morin, R.S., 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can. J. For. Res. 41, 2165–2175. http://dx.doi.org/10.1139/x11-138

Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx.doi.org/10.1139/cjfr-2014-0111.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1996. The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley and Sons, New York, NY.

Tardif, J., Bergeron, Y., 1997. Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. Can. J. For. Res. 27, 108–116. http://dx.doi.org/10.1139/x96-150.

Tardif, J., Bergeron, Y., 1993. Radial growth of *Fraxinus nigra* in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. J. Veg. Sci. 4, 751–758. http://dx.doi.org/10.2307/3235611.

Waring, K.M., O'Hara, K.L., 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. For. Ecol. Manag. 209, 27–41. http://dx.doi.org/10.1016/j.foreco.2005.01.008.

Chapter 2

The influences of competition and climate on tree growth vary with waterlogging stress in *Fraxinus nigra* wetland forests in northern Minnesota, USA

Christopher E. Looney [a, 1], Anthony W. D'Amato [b], Shawn Fraver [c], Brian J. Palik [d], Lee E Frelich [a]

[a] University of Minnesota, Department of Forest Resources, St. Paul, MN 55108, USA

[b] University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05095, USA

[c] University of Maine, School of Forest Resources, Orono, ME 04469

[d] USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA

1 Introduction

The performance of tree species along environmental stress gradients can provide insights into the controls on forest community organization (Keddy, 2001). Where climate is marginal for forest cover, topographic variation in soil moisture can create stress gradients with profound implications for tree growth and forest composition (Dymond et al., 2015). This effect may be especially dramatic in wetland forests, where even slight topographic changes can greatly affect tree exposure to waterlogging stress (Dudek et al., 1998) due to alterations in soil structure, aeration, and chemistry associated with inundation (Kozlowski, 1997). Topographic variation can also influence plant competition and may even shift plant interactions along an abiotic gradient from competition to facilitation (Callaway, 2007). Whether this influence extends to tree competition is unclear, as studies examining tree-to-tree interactions have focused with mixed results on mountain gradients (Coomes and Allen, 2007; Wilson, 1991). After correcting for variations in site productivity, Wilson (1991) found no differences in the importance of competition along an elevational gradient in Australian *Eucalyptus* forests. In contrast, Coomes and Allen (2007) found that competition for light decreases while competition for soil nutrients increases with elevation in New Zealand *Nothofagus solandri* Hook. (mountain beech) forest. No studies have examined the effect of environmental gradients on tree competition in wetland forests, despite the potential for similar dynamics at finer scales.

North American *Fraxinus nigra* Marsh. (black ash) wetland forests range from southeastern Canada (Scott, 1995) to the western Great Lakes region of the U.S.

(Erdmann et al., 1987). In the post-glacial topographic setting of northern Minnesota, *F. nigra* occurs within an environmental gradient between mesic uplands and wet peat-influenced bottomlands (Heinselman, 1963; MNDNR, 2003). At the mesic-to-moist upland margins of its habitat, *F. nigra* occurs with hardwoods such as *Acer saccharum* Marshall (sugar maple) and *Tilia americana* L. (American basswood), *Populus tremuloides* Michx. (quaking aspen), and *Betula* (birch) spp. (Heinselman, 1963; MNDNR, 2003). At the wet bottomland margins, *F. nigra* is associated with the coniferous species, *Thuja occidentalis* L. (northern white-cedar; Heinselman, 1963; MNDNR, 2003). Variation in the traits of these *F. nigra* associated species suggests differences in waterlogging stress may account for the dominance of *F. nigra* at the center of this moisture gradient (Keddy and MacLellan, 1990).

Previous studies suggest competition from upland species may help relegate *F. nigra* to marginal, hydric sites (Keddy and MacLellan, 1990). However, the importance of competition in structuring tree communities in *F. nigra* forests is unresolved. To date, studies of competition in *F. nigra* forests have focused on largely monospecific stands and have reached conflicting conclusions (Benedict and Frelich, 2008; Looney et al., 2016). Based on a simple measure of stand density, Benedict and Frelich (2008) found that *F. nigra* growth was higher at upland sites but that tree competition had little influence on the growth of the species at either upland or lowland sites. A subsequent study that included both stand density and the relative size and distance of neighboring trees found competition was generally an important limitation on *F. nigra* growth, with

the effect weaker on wetter sites, raising the possibility that tree-to-tree interactions vary between *F. nigra* sites (Looney et al., 2016).

Prior studies also found *F. nigra* growth is sensitive to climate (Tardif and Bergeron, 1997, 1993). *Fraxinus nigra* growth on a floodplain in a Quebec boreal forest responded negatively to spring flooding and positively to late-summer precipitation (Tardif and Bergeron, 1993), while sensitivity to spring precipitation appeared to increase with site flooding (Tardif and Bergeron, 1993). *Fraxinus nigra* growth at a drier, upland site showed temperature sensitivity suggestive of summer drought stress, whereas the bottomland conifer, *T. occidentalis* appeared sensitive to summer drought on both floodplain and upland sites (Tardif and Bergeron, 1997), suggesting growth-climate relationships may differ between *F. nigra* and associated species. Additional research is needed to assess tree growth at both upland and bottomland sites to clarify how climatic limitations vary by species within *F. nigra* wetland forests.

Fraxinus nigra forests are threatened by the invasive insect, emerald ash borer (*Agrilus planipennis* Fairmaire, EAB). EAB causes lethal girdling damage to North American ash species and has resulted in greater than 90% *Fraxinus* spp. mortality near the invasion epicenter (Iverson et al., 2016). A thorough understanding of black ash forest ecology is needed to inform the design of effective strategies to maintain post-EAB forest function (Waring and O'Hara, 2005). Toward this end, we investigated the influence of competition and climate on tree growth at the drier and wetter margins of a gradient of waterlogging stress in northern Minnesota *F. nigra* wetland forests. Using a retrospective tree-ring study, we examined the growth of *F. nigra* in association with *T. americana* at

two mesic sites, *P. tremuloides* at two moist sites, and *T. occidentalis* at two wet sites. Our purpose was to extend existing research in order to ascertain (1) how the influences of climate and competition vary by species in *F. nigra* forests, and (2) whether the importance of these factors shifts with topography-induced changes in waterlogging stress in a wetland forest setting.

2 Materials and Methods

2.1 Site description

We examined six mixed-species *F. nigra* stands in the Chippewa National Forest in northern Minnesota, USA (Figure 1). The climate is continental, with most precipitation occurring from May through September (PRISM Climate Group, 2015). Mean 1981-2010 temperatures for January and July were -13.7 and 16.5°C, respectively, and mean precipitation totaled 742 mm yr^{-1} (PRISM Climate Group, 2015).

We examined stand data in the U.S. Forest Service FSVEG Database (accessed 5/21/2014) to identify potential sites for sampling that contained a minimum of 7 m^2 ha^{-1} of *F. nigra* basal area (BA), together with a minimum of 7 m^2 ha^{-1} BA for at least one associated tree species. Because our initial surveys found that such sites were scarce, we accepted sites that contained a minimum of 30 trees with a diameter at breast height (DBH) ≥ 10 cm of *F. nigra* and at least one associated tree species. The most common *F. nigra* associated tree species included the upland hardwoods: *A. saccharum, T. americana,* and *P. tremuloides,* as well as the bottomland conifer, *T. occidentalis.* From these potential stands, we selected for sampling two sites (Round Lake and Wilderness

Lake) on which *A. saccharum, T. americana,* and *F. nigra* were co-dominant; two sites (Kupcho Run and Third River) on which *P. tremuloides* and *F. nigra* were co-dominant; and two sites (Pigeon Lake and Virgin Lake) on which *T. occidentalis* and *F. nigra* were co-dominant. Other species present at one or more of the sites included *Betula alleghaniensis* Britton (yellow birch) and *Fraxinus pennsylvanica* Marsh. (green ash). Total BA for all species sampled ranged from 21.8 m^2 ha^{-1} at Third River to 54.5 m^2 ha^{-1} at Virgin Lake (Table 1).

Soil type varied across the study sites (Table 1). We observed seasonal ponding into June at Round Lake and Wilderness Lake, into early July at Third River and Kupcho Run, and into mid-August at Pigeon Lake and Virgin Lake. Therefore, to better determine site moisture conditions, we calculated mean 8-directional contributing area for each site (Taborton, 2015), based on a pit-filled, 1/3 arc-second digital elevation model (U.S. Geological Survey, 2016). This metric calculates the area of adjacent land contributing water to a given point. Based on these calculations, we classified Round Lake and Wilderness Lake as mesic, Third River and Kupcho Run as moist, and Virgin Lake and Pigeon Lake as wet (Table 1).

2.2 Field data collection

We used QGIS 2.8 (Quantum GIS Development Team, 2014) to randomly generate a single initial sampling point per stand. We relocated sampling points within stands when the initial point fell within areas deficient in either *F. nigra* or associated species. In summer 2014, we installed a single 50 x 70 m (0.35 ha) plot per stand. We

assessed all trees ≥ 10.0 cm DBH within each plot for species, DBH, status (dead or living), stem Cartesian (x and y) coordinates, and crown class (Oliver and Larson, 1996). We initially sampled every third tree for growth by collecting a single increment core at 1.3m above ground level, to pith when possible. We later augmented this sample to achieve at least 30 trees of each major species per site. Cores were collected from all directions to reduce the risk of introducing systematic bias. In addition to *F. nigra,* which was sampled on all sites, sampled species included *A. saccharum* and *T. americana* at Round Lake and Wilderness Lake, *P. tremuloides* at Kupcho Run and Third River, and *T. occidentalis* at Pigeon Lake and Virgin Lake. We did not sample *F. pennsylvanica* given that, with the exception of *F. nigra,* our interest was on species unsusceptible to EAB.

2.3 Sample preparation

We prepared increment cores for analysis by drying, mounting, and progressively sanding to a fineness of up to 1500 grit (Speer, 2010). Prepared cores were scanned on an Epson V600 flatbed scanner and measured for annual ring widths using Cybis CooRecorder image analysis software (Larsson, 2014). We used the COFECHA program (Holmes, 1983) to verify cross-dating. While we sampled *A. saccharum,* we excluded this species from further analysis, as rot and fine ring structure confounded accurately distinguishing annual rings. Frequent rot in other species also resulted in partial cores that prevented estimation of inside-bark radius (Frelich, 2002). Given the minimal slopes of the study sites and random direction of core sampling, lack of correction for tree growth

asymmetry likely increased variability but did not introduce systematic bias in growth estimates.

For growth and competition modeling, we converted raw ring widths to basal area increment (BAI). We calculated BAI inward from the most recent year of growth due to frequent heart rot, using regional bark thickness equations (Dixon and Keyser, 2008) to calculate inside-bark diameter. We used the dplr package (Bunn, 2008) for R (R Core Team, 2016) to calculate BAI, as well as to standardize series and develop chronologies. For the analysis of growth-climate relationships, raw ring widths were standardized using 50-year splines with a wave cutoff of 0.5 (Table 2). *Populus tremuloides* at Third River was excluded due to the lack of series extending earlier than 1974. In preparation for statistical analysis, a single chronology was calculated for each species by site. We did not attempt to pool sites by moisture conditions during chronology development, as previous research suggests cross-dating of this species is sensitive to topographic position (Tardif and Bergeron, 1997). Prewhitened (residual) series were used for chronology development to remove the effects of serial autocorrelation.

2.4 Analysis

2.4.1 Growth and competition

Since prior research suggests neighborhood competition indices may reveal evidence of competition in *F. nigra* forests (Looney et al., 2016) that may be otherwise obscured when using traditional stand-level density metrics such as basal area (Benedict and Frelich, 2008), we compared three competition indices ranging from highly size-

asymmetric to size symmetric. Size asymmetric indices include information about competitor size relative to target trees and assume larger competitor trees have a disproportionately high influence on the growth of the smaller target tree (Larocque, 2002; Schwinning and Weiner, 1998). In contrast, size symmetric indices consider absolute size of competitor trees irrespective of target tree size and assume growth responds proportionally (Larocque, 2002). The first index, CI-1, is a sum of neighbor stem diameters, which is size-symmetric in that target tree diameter is not considered:

$$CI\text{-}1_i = \sum_{j=1}^{n} d_j$$

where $CI\text{-}1_i$ is the competition index (CI) for the individual target tree ($_i$) and d_j is the diameter(d) of a given competitor (*j).* The second index, CI-2, divides individual neighbor diameter by the diameter of the target tree and models competition as size-asymmetric (trees larger than the target tree disproportionately influence growth):

$$CI\text{-}2_i = \sum_{j=1}^{n} \frac{d_j}{d_i}$$

where symbols are as in CI-1, with the addition of d_i, the diameter of target tree (*i).* The third index, CI-3, squares the size ratio of CI-2 and is thus more highly size-asymmetric:

$$CI\text{-}3_i = \sum_{j=1}^{n} \left(\frac{d_j}{d_i}\right)^2$$

where symbols are as per CI-1 and CI-2. CI-1 and CI-2 were adapted from distance-dependent indices numbered CI-9 and CI-12, respectively, in Rouvinen and Kuuluvainen

(1997). CI-2 corresponds to Lorimer's index (Lorimer, 1983). For simplicity, all three of these indices were distance-independent (competitor trees not weighted by distance from target tree), as Looney et al. (2016) found indices weighting competitor influence by distance generally predicted *F. nigra* growth less well than distance-independent alternatives.

We used stem-mapped coordinates to define 5-m-radius neighborhoods around trees sampled for growth analysis. These neighborhoods were then used to calculate CI for each target tree. We did not buffer sampled trees from plot edges to avoid bias from unmeasured competitors outside the plot, as this would have greatly reduced the number of trees available for study. Instead, we estimated the unmapped portions of edge tree neighborhoods by dividing the total measured CI of each edge tree by the proportion of its neighborhood falling within the stem map. For example, a target tree on a stem map corner would have 25% of its neighborhood falling within the stem map, with the adjustment equal to the sum of measured CI/0.25. We did not investigate larger tree neighborhoods, as the proportion of trees requiring edge correction rapidly rose with neighborhood radius. Tree neighborhoods were defined using buffering and intersection operations in GIS (Quantum GIS Development Team, 2014).

We modeled the effects of competition on tree growth using linear modeling. Because sample sizes of cored species within sites were sometimes low (<30), we pooled sites to increase statistical power, based on moisture conditions: Round Lake and Wilderness Lake = mesic, Third River and Kupcho Run = moist, and Virgin Lake and Pigeon Lake = wet (Table 1). In addition to CI, predictors for all species included DBH

and the CI x DBH interaction. Previous research suggests these additional predictors can have greater influence on growth in *F. nigra* swamps than that of the main effect of CI (Looney et al., 2016), and we sought to control for variation in mean tree size between sites. Given the distribution of species across the study sites, we were able to develop growth models for *F. nigra* across all sites and moisture conditions, *T. americana* at the two mesic sites, *P. tremuloides* at the two moist sites, and *T. occidentalis* at the two wet sites. Because *F. nigra* occurred on all sites, we also include the main effect of moisture condition and its interactions with CI and DBH as potential predictors for this species only.

For each species, we developed a set of candidate growth models. We began with a saturated model including all main effects and interactions, from which we derived simpler competing models. We used the information-theoretic approach to evaluate the strength of evidence for each model using AIC (Burnham and Anderson, 2003). Candidate models within 8 AIC of the best-supported model were included within the model confidence set for each species (Burnham and Anderson, 2003). We used 20-year average BAI (1994-2013) for the response variable, based on the results of previous studies that found this window was most effective in eliminating the short-term variability in growth that may be associated with climate and stand dynamics (Aakala et al., 2013; Looney et al., 2016). We did not examine longer periodic averages, as ingrowth and mortality would have created increasing disparities between present (2014) tree neighborhoods and initial conditions. To meet model assumptions, we log-transformed BAI for all species, as well as DBH for *P. tremuloides.* All other predictors were left on

their original scales. We also centered and scaled BAI, DBH, and CI to reduce multicollinearity and compare the effects of predictors on a common scale. Adjacent trees may show similar growth as a result of shared disturbance histories or microsite characteristics, which can be controlled by modeling spatial autocorrelation (Aakala et al., 2013). Spatial autocorrelation was, therefore, modeled in the residuals by fitting an exponential variogram to each model. We used generalized least-squares modeling in the nlme package (Pinheiro et al., 2016) for R (R Core Team, 2016), offsetting coordinates by site geographic location to stratify autocorrelation estimates. We included intercept-only null models to assess whether spatial autocorrelation alone was a plausible explanation for observed growth patterns. We used the lsmeans package (Lenth, 2016) to investigate interaction effects where present. We used a significance level of $\alpha = 0.05$ for all growth-competition models, but restricted the use of significance testing to describing the terms of models with high AIC support.

2.4.2 Growth-climate relationships

We examined relationships between growth and interannual climatic variation for *F. nigra, T. americana, P. tremuloides,* and *T. occidentalis*. We restricted this analysis to the 1944-2013 period, given that sample depth prior to 1944 was limited by the relatively young age of trees at sites such as Round Lake, Wilderness Lake, and Kupcho Run (Table 2). We used mean monthly temperature and precipitation data as indicators of past climate (PRISM Climate Group, 2015). We used seasonal correlation analysis (seascorr; Meko et al., 2011; Zang and Biondi, 2015), which calculates simple and partial

correlations between tree ring chronologies and monthly climate data, to analyze relationships between annual growth and monthly climate records. This technique permits the investigation of climate integrated over periods of multiple months, or "seasons," which may be more influential in determining climatic effects on tree growth than individual monthly fluctuations (Meko et al., 2011). The significance of correlations between growth and seasonal variables were tested using exact simulation (Percival and Constantine, 2006). We set the window for analysis from August of the preceding year to September of the current year and used a season length of 3 months, e.g., a significant test result for June precipitation would indicate that April-June precipitation significantly influenced growth. Seasonal precipitation was used as the primary variable (given our focus on waterlogging) and analyzed with simple Pearson correlations to growth, while mean temperature was set as the secondary variable and analyzed in terms of partial correlations, limiting the potential influence of temperature intercorrelations with precipitation. We used a more stringent significance level ($\alpha = 0.01$) for the climate analysis, given the large number of significance tests involved and the seascorr procedure's lack of built-in error inflation adjustments (Meko et al., 2011).

3 Results

3.1 Growth and competition

Over the 1994-2013 period, mean *F. nigra* basal area increment (BAI) was highest on the mesic sites (6.8 ± 0.5 cm^2 yr^{-1}) and lowest on the moist sites (4.4 ± 0.3 cm^2 yr^{-1}), with growth on the wet sites (6.7 ± 0.5 cm^2 yr^{-1}) nearly equal to that of the mesic

sites. *Tilia americana* growth averaged 9.3 ± 0.8 cm^2 yr^{-1} on the mesic sites, *P. tremuloides* growth averaged 12.7 cm^2 yr^{-1} on the moist sites, and *T. occidentalis* growth averaged 7.4 ± 0.6 cm^2 yr^{-1} on the wet sites.

The best-supported (confidence set ΔAIC < 8) competition model for *F. nigra* included DBH, size-asymmetric CI-2 as a main effect, and the interaction between CI-2 and moisture condition, while the second, less-plausible model (confidence set ΔAIC <8) also included the interaction of CI-2 with DBH (Table 3). Based on the best-supported model, increasing competition appeared to have the most negative effect on *F. nigra* growth on the mesic sites, a moderately negative effect on the moist sites, and no effect on the wet sites (Figure 2). When holding inter-site variations in CI and DBH constant at their study-wide means, the mean growth rate of *F. nigra* did not appear to vary significantly in response to site moisture condition (Figure 2). We found no evidence of three-way interactions between DBH, CI, and moisture condition.

For *T. americana* growth on the mesic sites, a model including DBH as the sole predictor had greatest AIC support, while a candidate model with moderate AIC support (Δ AIC =3.8) included the strongly size-asymmetric CI-3 as a main effect (Table 3). The only plausible model of *P. tremuloides* growth on the moist sites included size-asymmetric CI-2 as a main effect and an interaction with DBH (Table 3). Model comparisons for *T. occidentalis* growth on the wet sites were less conclusive. The best-supported growth model for *T. occidentalis* included DBH and strongly size-asymmetric CI-3 as main effects, while a nearly equivalent model (Δ AIC=0.80) added an interaction

effect between DBH and CI-3 (Table 3). A model including DBH as the sole predictor of *T. occidentalis* growth also had substantial AIC support (Δ AIC = 1.8; Table 3).

3.2 Growth-climate relationships

Among the detrended tree ring series used in growth-climate chronologies, interseries correlations ranged from 0.33 for *T. americana* on the two mesic sites to 0.62 for *P. tremuloides* on the moist Kupcho Run site (Table 2). For the 1944-2013 period, the expressed population signal (EPS) was above 0.85 for all species, except for *T. americana,* which had an EPS of 0.60 and 0.71 at mesic Round Lake and Wilderness Lake, respectively (Table 2). Despite the lower EPS of *T. americana* chronologies, we opted to proceed with growth-climate analysis of this species with the caveat that individual-tree fluctuations may obscure group-level climate signals (Speer, 2010).

We found that, where significant, *F. nigra* growth responded positively to 3-month precipitation, with relationships shifting by site (Figure 3). On the mesic sites, *F. nigra* growth was positively influenced by precipitation that fell in early winter (ending in current January and February) and current spring/summer (ending in June and July) at Round Lake, while preceding fall precipitation (ending in December) positively influenced growth at Wilderness Lake. On the moist sites, *F. nigra* growth was positively influenced by preceding summer precipitation (ending in August and September) and current summer precipitation (ending in July) at Third River, while we found no significant correlation between precipitation and *F. nigra* growth at Kupcho Run. On the wet sites, *F. nigra* growth was positively influenced by current spring precipitation

(ending in June) at Pigeon Lake and by current spring/summer precipitation (ending in May, June, and July) at Virgin Lake.

Significant partial correlations between *F. nigra* and 3-month temperature were negative and restricted to fewer sites than direct correlations with precipitation (Figure 3). On the mesic sites, current spring temperatures (ending in May and June) were significantly correlated with reduced *F. nigra* growth at Wilderness Lake, while Round Lake showed no significant *F. nigra* growth-temperature relationships. On the moist sites, preceding summer temperatures (ending in August) were significantly correlated with reduced *F. nigra* growth at Third River, while Kupcho Run showed no significant *F. nigra* growth-temperature relationships. On the wet Kupcho Lake site, preceding summer temperatures (ending in September), winter temperatures (ending in current January, February, and March), and current spring temperatures (ending in June) were negatively correlated with *F. nigra* growth. *Fraxinus nigra* growth at Virgin Lake did not vary significantly with temperature.

Growth-climate relationships in other species were less numerous, in part reflecting the restriction of these species to fewer and topographically similar sites. We did not find any significant direct correlations between growth and seasonalized 3-month precipitation for *T. americana* on the mesic sites, *P. tremuloides* on the moist sites, or *T. occidentalis* on the wet sites (Figure 4). We also found no significant growth-temperature relationships for *P. tremuloides* or *T. occidentalis*. On the wet sites, we found a significant negative partial correlation between *T. occidentalis* growth and preceding summer temperatures (ending in September at Pigeon Lake and August at Virgin Lake).

4 Discussion

4.1 Growth and competition

Fraxinus nigra had the slowest growth of all species across the topographic gradient of waterlogging stress. We found *F. nigra* growth was slower than that of either *T. americana* on the mesic sites or *P. tremuloides* on the moist sites. On the wet sites, *F. nigra* grew more slowly than *T. occidentalis*, which is a generally slow-growing species (Hofmeyer et al., 2009a), although slightly faster radial growth in *T. occidentalis* may potentially be offset by greater taper compared with *F. nigra* and render these species similarly productive (Hofmeyer et al., 2009a). While greater waterlogging stress typically reduces the rate of tree growth (Megonigal et al., 1997), *F. nigra* growth did not significantly differ with site moisture conditions, after adjusting for the influences of tree size and competition. This finding contrasts with that of Benedict and Frelich (2008), who found *F. nigra* grew more rapidly in uplands when the influences of climate and competition were not considered.

Our finding that growth was higher in associated upland species compared with *F. nigra* suggests that *F. nigra* may be relegated to hydric sites in part by competition. While mean *F. nigra* growth did not vary by moisture condition, the influence of competition appeared to shift from important on the mesic and moist sites to unimportant on the wet sites. This finding is consistent with previous research that suggests *F. nigra* growth may be limited by competition from neighboring species at the drier margins of its habitat (Keddy and MacLellan, 1990). The growth response of *F. nigra* to competition

appeared most pronounced on the mesic sites, while competition appeared to have a negligible influence on *F. nigra* growth on the wet sites, even after accounting for variation in tree size. Our findings for this wetland system are at odds with those of previous studies of upland forests that suggest the general importance of competition varies little across a wide range of site productivity (Jack and Long, 1996; Wilson, 1991). In keeping with Rebertus et al. (1991), our results suggest that in the absence of disturbance the long-term persistence of mid-tolerant, slow-growing species such as *F. nigra* may be most feasible on sites with high abiotic stress.

Variation in *F. nigra* sensitivity to competition may reflect differences in competition symmetry and/or species composition between moisture conditions. Across all moisture conditions tested, *F. nigra* competition was best-modeled using the size-asymmetric CI-2, which suggests that trees may compete predominantly for light rather than for soil resources (Weiner, 1990). Plant competition is theorized to shift from above-ground competition for light (size-asymmetric) to below-ground competition for soil resources (size-symmetric) with increasing stress (Tilman, 1982), a pattern that has been reported in at least one observational upland forest study (Coomes and Allen, 2007). However, support for *F. nigra* models using the size-symmetric CI-1 and highly asymmetric CI-3 was invariably low, suggesting competition symmetry may have been relatively unaffected by increasing waterlogging stress. While our results are consistent with those of a previous study that found *F. nigra* growth appears to be most sensitive to size-asymmetric competition (Looney et al., 2016), individual species contributions to the competition index suggest traits of competing species may also have altered competition

intensity along the moisture gradient, both for *F. nigra* and the other species examined (data not shown).

For the mesic hardwoods, *T. americana* and *P. tremuloides*, DBH was a strong predictor of growth, with *T. americana* growth on the mesic sites most parsimoniously modeled using DBH as the sole predictor. Cole and Lorimer (1994) also found that diameter-based competition indices predicted the growth of *T. americana* poorly, with diameter alone the strongest predictor of growth. Growth of *P. tremuloides* on the moist sites was also strongly influenced by DBH, which interacted with the size-asymmetric CI-2 so that trees of this species appeared to decline slightly in sensitivity to competition with size. While Coates et al. (2009) found the sensitivity of *P. tremuloides* to competition increases with size, the authors examined stands that were younger (<25 yr age) than those on our study sites. *Populus tremuloides* does not appear to dramatically decline in competitive ability and growth efficiency with maturity (Binkley et al., 2006).

On the wet sites, the apparent sensitivity of *T. occidentalis* contrasts with the apparent insensitivity of *F. nigra* to competition. When compared with the other species examined, *T. occidentalis* typically had intermediate or suppressed crown condition (data not shown), reducing the potential for this species to compete with *F. nigra* for light. Yet the effect of competition on *T. occidentalis* growth appears minor in comparison with the effect of target tree size. Previous research suggests the growth of *T. occidentalis* does not vary by canopy position (Hofmeyer et al., 2009b), nor does it consistently improve following silvicultural treatments that reduce competition (Hofmeyer et al., 2009a). Size-

asymmetric competition with hardwoods may play a role in restricting *T. occidentalis* to more hydric sites but appears less influential to *T. occidentalis* than to *F. nigra* growth.

4.2 Growth-climate relationships

Preceding-year precipitation was positively correlated with *F. nigra* growth at the mesic and moist margins of the waterlogging gradient. On the mesic sites, *F. nigra* growth was positively influenced by early winter precipitation (ending in current-year January and February) at Round Lake and by preceding fall precipitation (ending in December) at Wilderness Lake. Preceding fall and early winter precipitation may promote early winter snowpack that protects fine roots from frost (Frey et al., 2004), although why this mechanism would be stronger on the mesic sites is unclear. On the moist Third River site, *F. nigra* growth increased significantly in response to preceding summer precipitation (ending in August and September). Tardif and Bergeron (1993) suggested precipitation late in the preceding summer may lead to the development of lammas shoots in *F. nigra*, influencing bud primordia and subsequent foliage production in this determinate-growth species. More broadly, the climate of the preceding growing season may increase carbohydrate reserves, which are especially important to earlywood formation in ring-porous species such as *F. nigra* (Tardif and Conciatori, 2006).

Current year spring/summer precipitation (ending in May, June and/or July) was positively correlated with *F. nigra* growth across the site moisture gradient, although the effect was present at only one mesic and one moist site. At mesic Round Lake and moist Third River, positive current-year growth-precipitation relationships in *F. nigra* resemble

those of other bottomland species such as *Juglens nigra* L. (black walnut) and *P. deltoides* Marsh. (eastern cottonwood) when subjected to drought stress (Dudek et al., 1998). In contrast, increased *F. nigra* growth on the two wet sites, where we observed surface water flow into late summer, may reflect inputs of water-borne nutrients (Megonigal et al., 1997).

Temperature negatively affected *F. nigra* growth at mesic Wilderness Lake, moist Third River, and wet Pigeon Lake. The most numerous relationships between *F. nigra* growth and temperature occurred at the wet Pigeon Lake site, where current-year temperatures significantly reduced growth for the three-month seasons ending in current-year January through March and current year June. While both Pigeon Lake and Virgin Lake were classified as wet sites, Pigeon Lake had only half the contributing watershed and, as a result, likely had less reliable summer soil moisture. High temperatures in winter and spring diminish snow packs, leading to reduced soil moisture and stream flow during the summer growing season (Yulianti and Burn, 1998). In addition, high water tables during the spring thaw may restrict rooting zones to shallow depths, with growing season declines in water table depth later exposing trees to drought stress (Girardin et al., 2001).

In contrast to *F. nigra,* the growth of *T. americana* on the mesic sites and *P. tremuloides* on the moist sites did not respond to either climate variable. The lack of sensitivity of *T. americana* and *P. tremuloides* to precipitation suggests mature trees (DBH $\geq$ 10 cm) of these species may be relatively unaffected by moisture conditions at the drier *F. nigra* forest margins. *Thuja occidentalis* growth on the wet sites showed no

significant correlations with precipitation but declined in response to preceding summer temperatures (ending in September at Pigeon Lake and August at Virgin Lake). Previous research found growth declines in *T. occidentalis* in response to late preceding summer temperatures (Jean and Bouchard, 1996), which may influence the carbohydrate reserves needed for growth (Tardif and Stevenson, 2001). Nevertheless, particularly at the Pigeon Lake site, growth of *T. occidentalis* appeared less constrained by climate than *F. nigra*, suggesting *T. occidentalis* may be the better-suited of the two species to heavy waterlogging stress.

5 Conclusions

The growth of *Fraxinus nigra* was the slowest of all species examined and did not vary across the topographic gradient of waterlogging stress, after correcting for the influences of competition and tree size. On the upland mesic and moist sites, *F. nigra* grew more slowly and appeared to be comparatively more sensitive to competition than *T. americana* and *P. tremuloides*, which suggests the associated species may outcompete *F. nigra* at the drier upland margins of the moisture gradient. On the wet bottomland sites, *F. nigra* showed slightly slower growth but lower sensitivity to competition than *T. occidentalis*, indicating *T. occidentalis* may be more limited by competition on hydric bottomland sites than *F. nigra*. For all species, competitive interactions appeared to be predominantly size-asymmetric, suggesting growth is primarily light-limited.

We found *F. nigra* growth responded positively to precipitation and negatively to temperature across the gradient of waterlogging stress. In contrast, we found no growth-precipitation relationships for any of the associated tree species, suggesting mature trees of these species are relatively unaffected by moisture conditions in their respective habitats at the *F. nigra* forest margins. The greater sensitivity of *F. nigra* to variations in precipitation likely plays a role in relegating *F. nigra* to moderately hydric, bottomland sites. The only associated species for which we found a growth-temperature relationship was *T. occidentalis,* for which preceding-year summer temperatures were negatively correlated with growth on the wet sites.

Mature *T. americana* and *P. tremuloides* appear climatically well-suited to the mesic and moist topographic margins of the *F. nigra* forests we studied, while mature *T. occidentalis* appears climatically well-suited to the very wet margins. These results suggest that management strategies to promote increased regeneration of these species could potentially aid in maintaining forest functions following the anticipated loss of *F. nigra* to EAB. However, the co-occurrence of *F. nigra* with *T. americana* and *P. tremuloides* on the drier sites is puzzling, given *F. nigra*'s relatively slower growth and greater sensitivity to competition. Environmental tolerances of seedlings often differ from those of mature trees (Shipley, 1999). Therefore, interspecific differences in natural regeneration success should be investigated as a possible explanation for the persistence of *F. nigra* with these species at the drier sites.

References

Aakala, T., Fraver, S., D'Amato, A.W., Palik, B.J., 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. For. Ecol. Manag. 308, 128–135. http://dx/doi.org/10.1016/ j.foreco. 2013. 07.057.

Benedict, M.A., Frelich, L.E., 2008. Site factors affecting black ash ring growth in northern Minnesota. For. Ecol. Manag. 255, 3489–3493. http://dx/doi.org/10.1016/ j.foreco.2008.02.029.

Binkley, D., Kashian, D.M., Boyden, S., Kaye, M.W., Bradford, J.B., Arthur, M.A., Fornwalt, P.J., Ryan, M.G., 2006. Patterns of growth dominance in forests of the Rocky Mountains, USA. For. Ecol. Manag. 236, 193–201. http://dx/doi.org/10.1016/ j.foreco.2006.09.001.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. http://dx/doi.org/10.1016/j.dendro.2008.01.002.

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Callaway, R.M., 2007. Interaction between Competition and Facilitation, in: Positive Interactions and Interdependence in Plant Communities. Springer. Dordrecht, The Netherlands, pp. 179–254.

Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130. http://dx/doi.org/10.1111/j.1365-2745.2008.01458.x.

Cole, W.G., Lorimer, C.G., 1994. Predicting tree growth from crown variables in managed northern hardwood stands. For. Ecol. Manag. 67, 159–175. http://dx/doi.org/ 10.1016/ 0378-1127(94)90014-0.

Coomes, D.A., Allen, R.B., 2007. Effects of size, competition, and altitude on tree growth. J. Ecol. 95, 1084–1097. http://dx/doi.org 10.1111/j.1365-2745.2007.01280.x.

Dixon, G.E., Keyser, C.E., 2008. Lake States (LS) Variant Overview: Forest Vegetation Simulator, Internal Rep. USDA Forest Service, Forest Management Service Center, Fort Collins, CO.

Dudek, D.M., McClenahen, J.R., Mitsch, W.J., 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. Am. Midl. Nat. 140, 233–244. http://dx/doi.org/10.1674/0003-0031(1998)140[0233:TGROPD]2.0.CO;2.

Dymond, S.F., D'Amato, A.W., Kolka, R.K., Bolstad, P.V., Sebestyen, S.D., Bradford, J.B., 2015. Growth-climate relationships across topographic gradients in the northern Great Lakes. Ecohydrology. http://dx/doi.org/10.1002/eco.1700.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115,.

Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge, UK.

Frey, B.R., Lieffers, V.J., Hogg, E. (Ted), Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. Can. J. For. Res. 34, 1379–1390. http://dx/doi.org/10.1139/x04-062.

Girardin, M.-P., Tardif, J., Bergeron, Y., 2001. Radial growth analysis of *Larix laricina* from the Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks. Écoscience 8, 127–138. http://dx/doi.org/10.1080/ 11956860. 2001.11682638.

Heinselman, M.L., 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz Region, Minnesota. Ecol. Monogr. 327–374. http://dx/doi.org/ 10.2307/1950750.

Hofmeyer, P.V., Kenefic, L.S., Seymour, R.S., 2009a. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. North. J. Appl. For. 26, 21–27.

Hofmeyer, P.V., Seymour, R.S., Kenefic, L.S., 2009b. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. North. J. Appl. For. 26, 68–75.

Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43: 69-78.

Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx/doi.org/10.1007/s10021-015-9929-y.

Jack, S.B., Long, J.N., 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. For. Ecol. Manag. 86, 205–220. http://dx/doi.org/ 10.1016/S0378-1127(96)03770-X.

Jean, M., Bouchard, A., 1996. Tree-ring analysis of wetlands of the upper St. Lawrence River, Quebec: Response to hydrology and climate. Can. J. For. Res. 26, 482–491. http://dx/doi.org/10.1139/x26-054

Keddy, P.A., 2001. Competition Gradients, in: Competition, Population and Community Ecology. Springer, Dordrecht, The Netherlands, pp. 281–315.

Keddy, P.A., MacLellan, P., 1990. Centrifugal organization in forests. Oikos 59, 75–84. http://dx/doi.org/10.2307/3545125.

Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. 17, 490. http://dx/doi.org/10.1093/treephys/17.7.490.

Larocque, G.R., 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. For. Sci. 48, 24–34.

Larsson, L.A., 2014. CooRecorder and Cdendro programs of the CooRecorder/Cdendro package. Cybis Elektronik.

Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. 69, 1–33. http://dx/doi.org/10.18637/jss.v069.i01.

Looney, C.E., D'Amato, A.W., Fraver, S., Palik, B.J., Reinikainen, M.R., 2016. Examining the influences of tree-to-tree competition and climate on size-growth

relationships in hydric, multi-aged *Fraxinus nigra* stands. For. Ecol. Manag. 375, 238–248. http://dx/doi.org/ 10.1016/j.foreco.2016.05.050.
Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. 6, 343–360. http://dx/doi.org/10.1016/ 0378-1127(83)90042-7.
Megonigal, J.P., Conner, W.H., Kroeger, S., Sharitz, R.R., 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy–stress hypothesis. Ecology 78, 370–384. http://dx/doi.org/10.1890/0012-9658(1997)078 [0370:APISFF]2.0.CO;2.
Meko, D.M., Touchan, R., Anchukaitis, K.J., 2011. Seascorr: A MATLAB program for identifying the seasonal climate signal in an annual tree-ring time series. Comput. Geosci. 37, 1234–1241. http://dx/doi.org/10.1016/j.cageo.2011.01.013.
MNDNR, 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, MN.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics: Updated Edition. John Wiley and Sons, Inc., New York, NY.
Percival, D.B., Constantine, W.L.B., 2006. Exact simulation of Gaussian time series from nonparametric spectral estimates with application to bootstrapping. Stat. Comput. 16, 25–35. http://dx/doi.org/10.1007/s11222-006-5198-0.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2016. nlme: Linear and nonlinear mixed effects models. https://CRAN.R-project.org/package=nlme (accessed 3.5.16).
PRISM Climate Group, 2015. PRISM climate data. Northwest Alliance Comput. Sci. Eng. http://www.prism.oregonstate.edu/recent/ (accessed 1.11.15).
Quantum GIS Development Team, 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rebertus, A.J., Burns, B.R., Veblen, T.T., 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. J. Veg. Sci. 2, 445–458. http://dx/doi.org/ 10.2307/3236026.
Rouvinen, S., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27, 890–902. http://dx/doi.org/10.1139/cjfr-27-6-890.
Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113, 447–455. http://dx/doi.org/ 10.1007/ s004420050397.
Scott, G.A.J., 1995. Canada's Vegetation: A World Perspective. McGill-Queen's Press, Montreal, Quebec.
Shipley, B., 1999. Testing causal explanations in organismal biology: Causation, correlation and structural equation modelling. Oikos 86, 374–382. http://dx/doi.org/ 10.2307/ 3546455.
Speer, J.H., 2010. Fundamentals of Tree-ring Research. University of Arizona Press, Phoenix, AZ.

Taborton, D., 2015. Terrain Analysis using Digital Elevation Models (TauDEM Version 5). Utah State University Hydrology Research Group. http://hydrology.usu.edu/taudem/taudem5/ index.html (accessed 12.4.16).
Tardif, J., Bergeron, Y., 1997. Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. Can. J. For. Res. 27, 108–116. http://dx/doi.org/ 10.1139/x96-150.
Tardif, J., Bergeron, Y., 1993. Radial growth of *Fraxinus nigra* in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. J. Veg. Sci. 4, 751–758. http://dx/doi.org/10.2307/3235611.
Tardif, J.C., Conciatori, F., 2006. Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, southwestern Quebec, Canada. Can. J. For. Res. 36, 2317–2330. http://dx/doi.org/10.1139/x06-133.
Tardif, J.C., Stevenson, D., 2001. Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. Dendrochronologia 19, 1–9.
Tilman, D., 1982. Resource competition and community structure. Monogr. Popul. Biol. 17, 1–296.
U.S. Geological Survey, 2016. The National Map: 3D Elevation Program (3DEP). http://nationalmap.gov/3DEP/3dep_prodserv.html (accessed 12.30.16).
Waring, K.M., O'Hara, K.L., 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. For. Ecol. Manag. 209, 27–41. http://dx/doi.org/10.1016/ j.foreco.2005.01.008.
Weiner, J., 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5, 360–364. http://dx/doi.org/ 10.1016/0169-5347(90)90095-U.
Wilson, S.D., 1991. Variation in competition in eucalypt forests: The importance of standardization in pattern analysis. J. Veg. Sci. 2, 577–586. http://dx/doi.org/ 10.2307/ 3236169.
Yulianti, J.S., Burn, D.H., 1998. Investigating links between climatic warming and low streamflow in the Prairie Region of Canada. Can. Water Resour. J. Rev. Can. Ressour. Hydr. 23, 45–60. http://dx/doi.org/10.4296/cwrj2301045.
Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436. http://dx/doi.org/10.1111/ecog.01335.

Table 1. Summary of cover, stand, and physical characteristics for six sites located in *Fraxinus nigra* forest in northern Minnesota, USA.

		Cover Type and Site					
		Mesic		Moist		Wet	
Measure	Species	Round Lake	Wilderness Lake	Third River	Kupcho Run	Pigeon Lake	Virgin Lake
BA (m^2 ha^{-1})	ACSA	3.4	8.2	0	0	0	0
	BEAL	0.9	2.6	0	0	0.2	2.2
	FRNI	4.5	8.7	8.3	8.4	27.5	26
	FRPE	5.9	2.6	5.3	4.8	0.7	0
	POTR	4.1	0.2	7.8	15.2	0	0
	THOC	0	0.2	0	0	10.1	25.6
	TIAM	8	10.1	0	1.5	0	0
	Other	2	1.2	0.5	1.7	1.2	0.7
	Total	28.9	34	21.8	31.7	39.7	54.5
% F. nigra		15.5	25.5	38.1	26.5	69.3	47.8
Trees ha^{-1}		645.7	702.9	605.7	777.1	525.7	960
QMD (cm)		23.9	24.8	21.4	22.8	31	26.9
Soil Classification		Mollic Psammaquent	Aqguic Glossudalf	Histic Humaquept	Histic Humaquept	Typic Haplosaprist	Typic Haplosaprist
Contributing area (ha)		0.3 ± 0.1	0.8 ± 0.2	1.3 ± 0.4	2.2 ± 1.3	133.5 ± 62.6	270.4 ± 86.7

Note: Species abbreviations are as follows: ACSA=*Acer saccharum*, BEAL=*Betula alleghaniensis*,FRNI=*Fraxinus nigra*, FRPE=*Fraxinus pennsylvanica*, POTR=*Populus tremuloides*, THOC=*Thuja occidentalis*, TIAM=*Tilia americana*. QMD=quadratic mean diameter. Contributing area=estimated adjacent land area (ha) from which water flows through the plot. Sites are arranged from left to right in order of increasing contributing area to represent the gradient of waterlogging stress.

Table 2. Selected characteristics of tree ring series by species, moisture condition, and site.

Species	Moisture condition	Site	Number of trees	DBH (cm)	BAI (cm^2 yr^{-1})	Interseries correlation	EPS
FRNI	mesic	Round Lake	26	20.3 ± 1.4	7.3 ± 1.0	0.51	0.89
FRNI	mesic	Wilderness Lake	27	20.5 ± 1.1	6.4 ± 0.8	0.42	0.87
FRNI	moist	Third River	33	17.2 ± 1.4	5.1 ± 1.0	0.44	0.85
FRNI	moist	Kupcho Run	39	16.7 ± 1.2	3.7 ± 0.5	0.59	0.95
FRNI	wet	Pigeon Lake	26	28.6 ± 2.2	8.1 ± 1.5	0.46	0.86
FRNI	wet	Virgin Lake	30	22.0 ± 1.5	5.7 ± 0.7	0.49	0.86
TIAM	mesic	Round Lake	18	24.4 ± 2.0	6.4 ± 1.0	0.33	0.60
TIAM	mesic	Wilderness Lake	25	27.3 ± 2.3	11.2 ± 1.6	0.33	0.71
POTR	moist	Third River	30	21.9 ± 1.2	11.6 ± 1.3	0.44	0.88
POTR	moist	Kupcho Run	30	24.5 ± 2.1	13.9 ± 2.2	0.62	0.90
THOC	wet	Pigeon Lake	26	31.7 ± 1.8	9.7 ± 1.5	0.44	0.86
THOC	wet	Virgin Lake	30	29.9 ± 1.5	5.8 ± 0.6	0.40	0.85

Note: Species name abbreviations are as per Table 1. Number of trees = number of trees cored; DBH = diameter at breast height; BAI = basal area increment; Interseries correlation = the mean correlation of an individual tree ring series with the master chronology; EPS = expressed population signal. Means ± standard errors are provided for DBH and basal area increment.

Table 3. Comparison of tree growth models in the model confidence set ($\Delta AIC \leq 8$) and null models for four northern Minnesota *F. nigra* forest species, *Fraxinus nigra* (FRNI), *Tilia americana* (TIAM), *Populus tremuloides* (POTR), and *Thuja occidentalis* (THOC).

Moisture Condition	Species	DBH	CI formula	CI	DBH x CI	Moisture Condition	Moisture x CI	AIC	Δ AIC	Evidence ratio
All	FRNI	0.73***	CI-2	-0.46***	---	*	***	283.82	0	1
All	FRNI	1.16***	CI-2	-0.14	0.2	N.S.	N.S.	289.7	5.88	18.92
All	FRNI	---	---	---	----	----	---	504.9	221.1	1.02E+48
Mesic	TIAM	0.67***	---	---	---	---	---	112.4	0	1
Mesic	TIAM	0.69***	CI-3	-0.02	---	---	---	116.2	3.8	6.69
Mesic	TIAM	---	---	---	---	---	---	146.5	34.1	2.54E+07
Moist	POTR	1.01***	CI-2	-0.1	0.15*	---	---	28.99	0	1
Moist	POTR	---	---	---	---	---	---	154.7	102.4	1.72E+22
Wet	THOC	0.88***	CI-3	-0.21**	---	---	---	69.6	0	1
Wet	THOC	0.86***	CI-3	0.04	-0.15*	---	---	70.4	0.8	1.49
Wet	THOC	0.68***	---	---	---	---	---	71.4	1.8	2.46
Wet	THOC	0.83***	CI-1	0.11	-0.12*	---	---	73.8	4.2	8.17
Wet	THOC	0.76***	CI-1	-0.1	---	---	---	75.2	5.6	16.44
Wet	THOC	---	---	---	---	---	---	128.8	59.2	7.16E+12

Note: See text for CI (competition index) formula. DBH (diameter at breast height), CI, and DBH x CI columns show standardized partial regression coefficients (beta weights) when present. Intercept-only null models indicated by blanks for all terms. Coefficients for the main effect of moisture condition and moisture condition x CI interaction are not available, as moisture condition was a nominal factor variable. Also provided are Akaike's information criterion (AIC) for model comparisons within species. Symbols are as follows: AIC, difference compared with best-fitting model (ΔAIC), evidence ratio. Akaike weights calculated for models within the confidence sets also incorporate null intercept models. *Significant at $p<0.05$; **$p<0.01$;***$p<0.005$

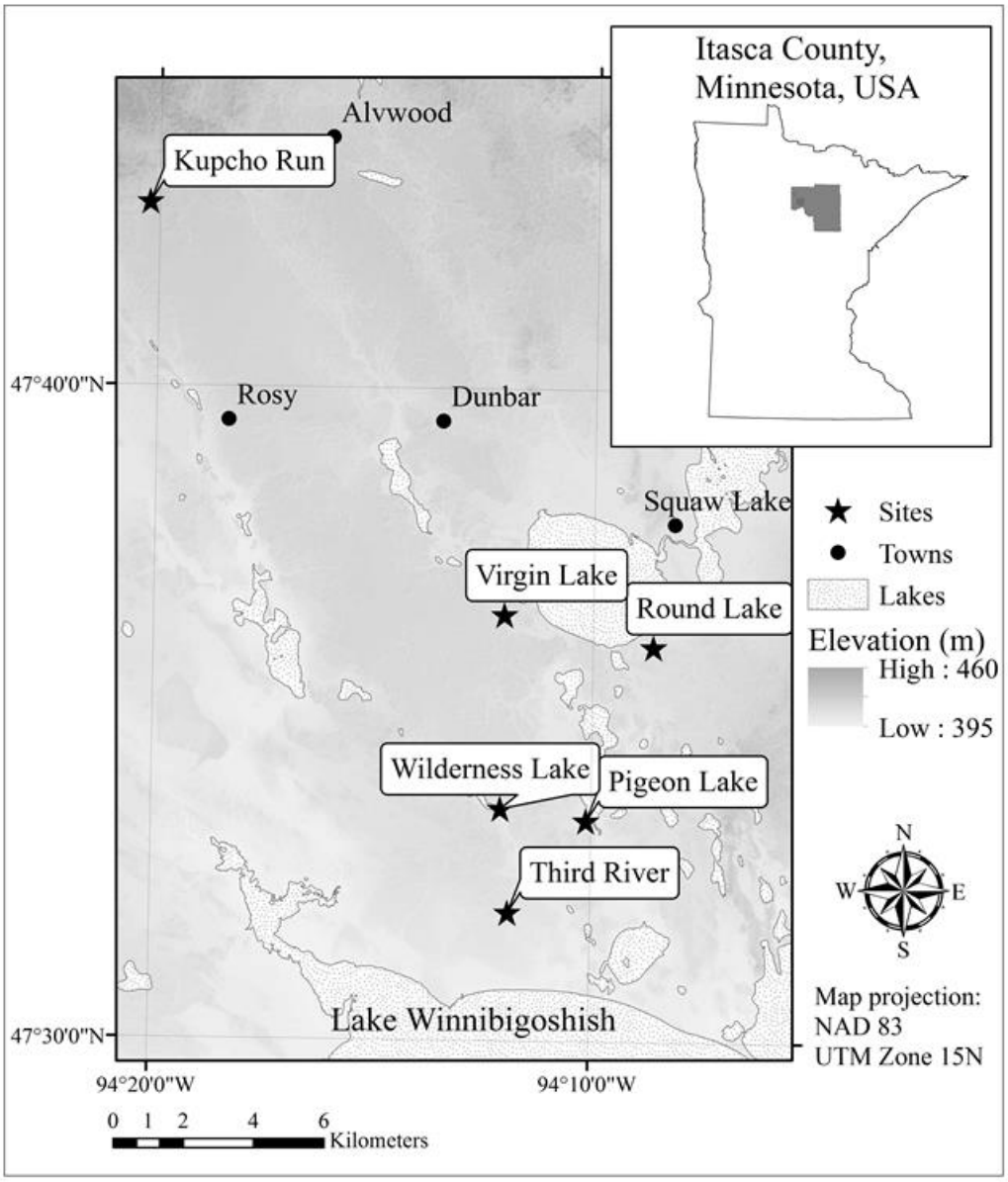

Figure 1. Locations of six *Fraxinus nigra* forest study sites in Itasca County, northern Minnesota, USA.

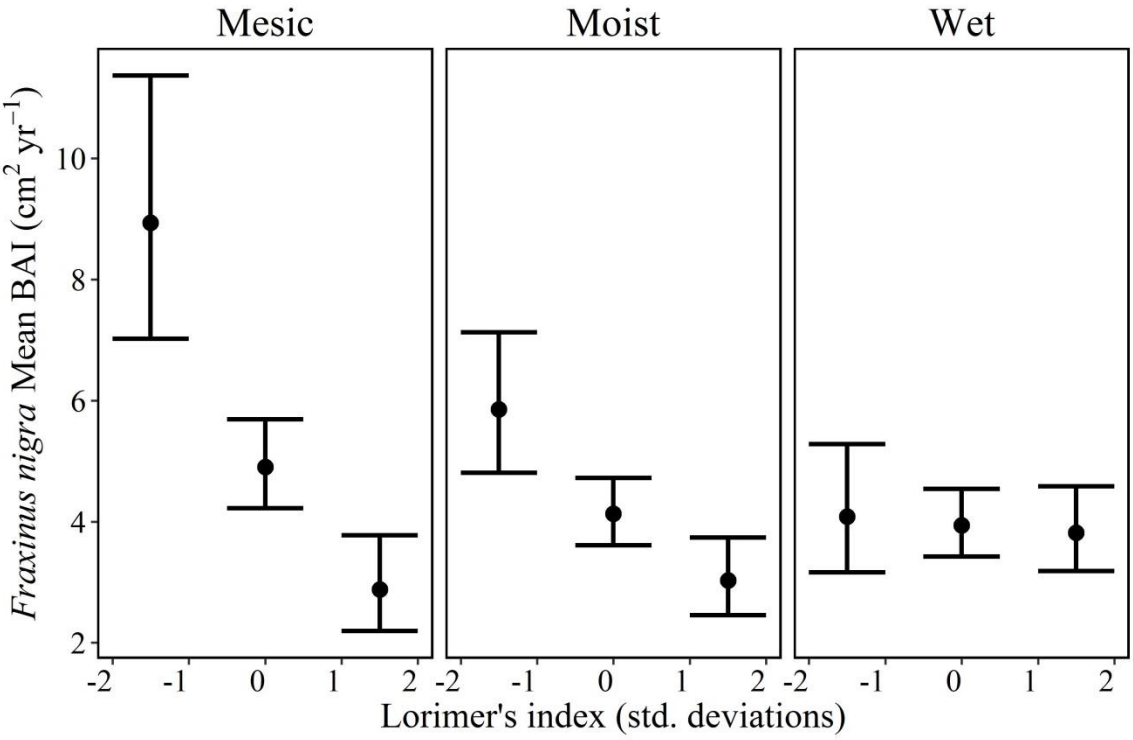

Figure 2. Plot illustrating the interaction effect of Lorimer's competition index and cover type on *Fraxinus nigra* basal area increment. Adjusted least-squares means and 95% confidence intervals of BAI (cm^2 yr^{-1}) are back-transformed from the log scale, holding tree diameter constant at its average. Basal area increment represents the annual average growth during the 1994-2013 period. Growth is calculated with Lorimer's index set at -1.5 (less competition), 0 (average competition), and 1.5 (more competition) standard deviations. Growth at 0 standard deviations represents mean *F. nigra* growth by moisture conditions, holding competition and diameter constant at their means.

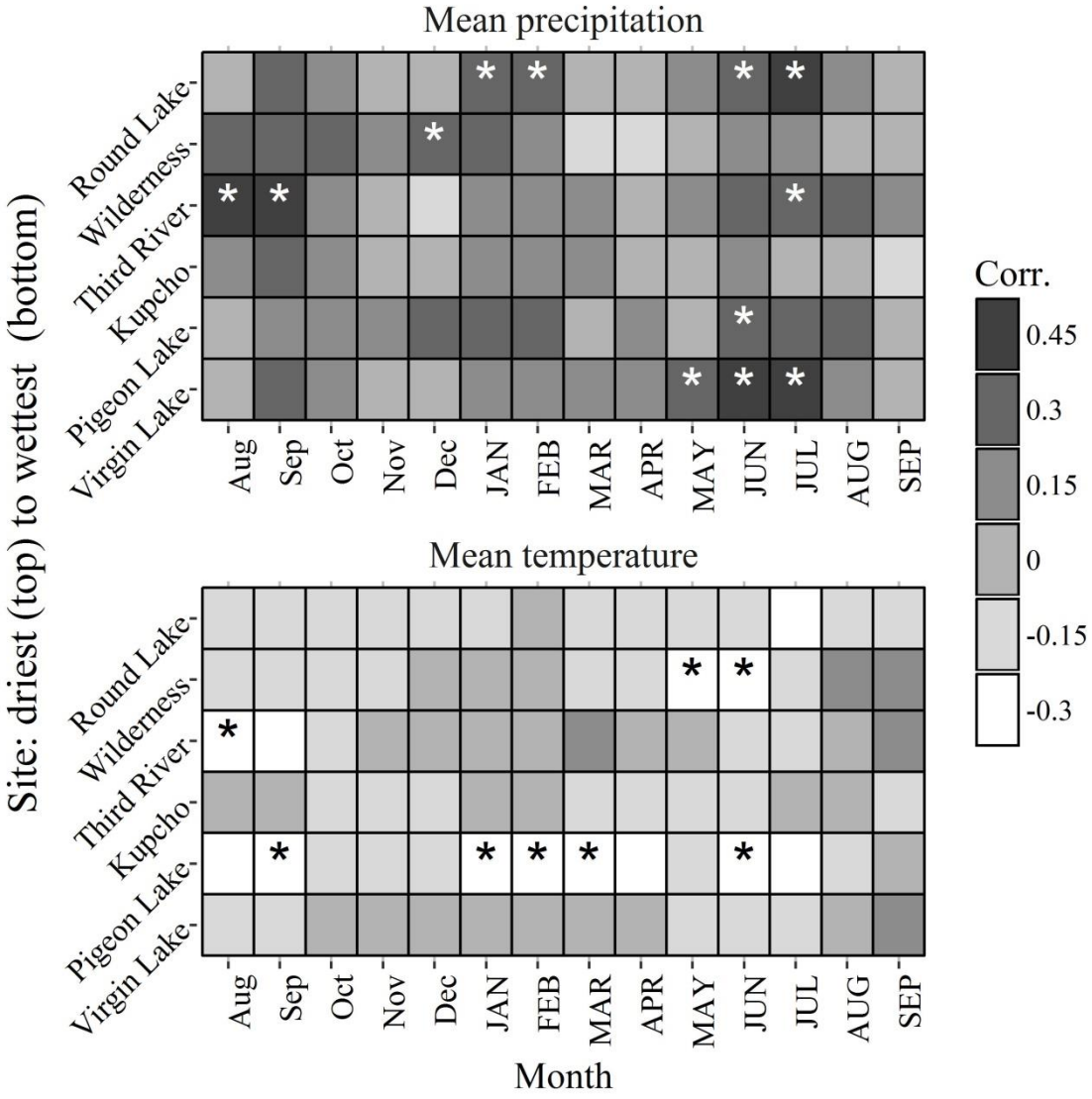

Figure 3. Raster plot showing relationship of *Fraxinus nigra* growth to precipitation and temperature at the *F. nigra* forest margins, based on seascorr results of 3-month integration periods. Sites are arranged to represent the waterlogging gradient, with most mesic at the top to wettest at the bottom. Species responses are organized by month along the x-axis, with lower-case letters designating months of the prior year, and upper-case letters months of the current year. Shading within cells shows the strength and direction of correlations (Corr.) between growth and climate variables. Simple Pearson correlations are used with precipitation, and partial correlations with temperature. Months in which a climate variable was significantly correlated with growth (alpha<0.01) are designated with a black or white asterisk, with different asterisk colors chosen for readability only.

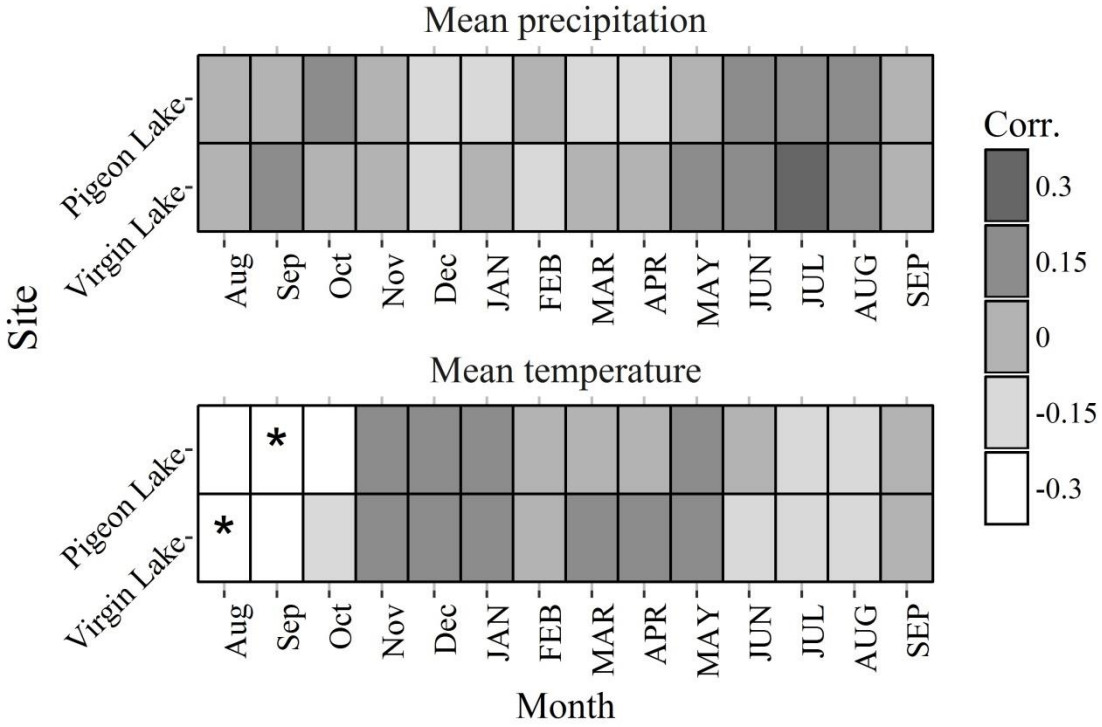

Figure 4. Raster plot showing relationship of *Thuja occidentalis* (THOC) growth to precipitation and temperature at the wet margins of *F. nigra* forest, based on seascorr results of 3-month integration periods. Sites are arranged to represent the waterlogging gradient, with the wetter plot at the bottom. Species responses are displayed as months along the x-axis, with lower-case letters designating months of the prior year, and upper-case letters months of the current year. Shading within cells shows the strength and direction of correlations (Corr.) between growth and climate variables. Simple Pearson correlations are used with precipitation, and partial correlations with temperature. Months in which a climate variable was significantly correlated with growth (alpha<0.01) are designated with a black or white asterisk, with asterisk colors chosen for readability only. Results for *Tilia americana* and *Populus tremuloides*, which were also tested, are not shown due to lack of significant correlations with any climate variable.

Chapter 3

Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer-threatened Fraxinus nigra forests in Minnesota, USA

Christopher E. Looney[a], Anthony W. D'Amato[b], Brian J. Palik[c], Robert A. Slesak[d]

[a] University of Minnesota, Department of Forest Resources, St. Paul, MN 55108, USA

[b] University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05095, USA

[c] USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA

[d] Minnesota Forest Resources Council, St. Paul, MN 55108, USA

Reprinted from Canadian Journal of Forest Research, Vol. 45, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer-threatened *Fraxinus nigra* forests in Minnesota, USA, pp. 1728-1738, © 2015 Christopher E. Looney, Anthony W. D'Amato, Brian J. Palik, Robert A. Slesak, with permission from Canadian Science Publishing. http://dx.doi.org/10.1139/cjfr-2015-0129.

1 Introduction

Fraxinus nigra Marsh (black ash) wetland forests in northern Minnesota, USA, are threatened by the introduced Asian insect, emerald ash borer (*Agrilus planipennis* Fairmaire (EAB), Pugh et al. 2011). First detected in southern Michigan in 2002, EAB has caused high mortality in *Fraxinus* populations in other areas of the Great Lakes region (Pugh et al. 2011). Control methods are constrained by lack of EAB resistance in North American *Fraxinus* spp. (Poland and McCullough 2006). Insecticides are effective but restricted to high-value urban trees, whereas wildland management to date has focused without success on quarantine to slow the pace of invasion (Poland and McCullough, 2006).

Tolerant of heavily saturated soils and seasonal ponding, *F. nigra* serves as a foundation species in northeastern Minnesota's expansive wetland forests (Telander et al., 2015). In other locations in North America, *F. nigra* is dominant at localized scales in heavily inundated swamp forests and poorly drained depressions (Cohen et al., 2014; Epstein et al., 2002; Scott, 1995), as well as occurring as an associated species in upland mixed-hardwood forests (Erdmann et al., 1987). As a foundation species in Minnesota, *F. nigra* plays an important role in regulating ecosystem processes by lowering water tables in summer through evapotranspiration (Telander et al., 2015). In this way, it aids the survival of associated tree species, while allowing a mixture of facultative and obligate wetland species to exist in the herbaceous understory (Lenhart et al., 2012). *Fraxinus nigra* forests support a wide variety of understory plant species and provide important habitat for large and small mammals, birds, amphibians, reptiles and arthropods (Gucker,

2005). *Fraxinus nigra* is culturally and economically important to northern Minnesota Native American tribes, who use its wood to weave their traditional baskets (Benedict and Frelich, 2008).

Kashian and Witter (2011) suggest that *Fraxinus* spp. regeneration in southern Michigan's upland, mixed-*Fraxinus* forests appears sufficient to offset EAB-related mortality, but post-EAB regeneration in *F. nigra*-dominated wetland forests may be considerably lower due to hydrological changes from the loss of the *F. nigra* overstory (Palik et al., 2012). A study that examined the effects of logging on *F. nigra* forests found that the loss of the overstory to clearcutting raised the water table and promoted growth of the herbaceous layer at the expense of tree regeneration (Erdmann et al., 1987). Even assuming ample *F. nigra* regeneration, it is uncertain whether the new trees will survive to maturity (Kashian and Witter, 2011). On sites near the southern Michigan epicenter of the North American EAB invasion, *F. nigra* and trees of other *Fraxinus* spp. with a diameter $\geq$ 2.5 cm (1 in) experienced a greater than 99% mortality rate between the estimated start of the outbreak in 1998 and 2010 (Herms and McCullough, 2014). Although the nearly pure *F. nigra* wetland forests of northern Minnesota (Minnesota Department of Natural Resources (MNDNR) 2003) differ dramatically from the mixed-species stands of southern Michigan (Cohen et al., 2014), such findings suggest that the continued spread of EAB could potentially result in large-scale loss of *F. nigra* from the extensive Minnesota wetland forests it presently dominates (Pugh et al., 2011).

In the event of such a worst case scenario, a possible management option is promoting increased regeneration of unsusceptible, alternative tree species to maintain

forest cover and ecosystem functions (Slesak et al., 2014). Tree species often associated with *F. nigra* in Minnesota include *Ulmus americana* L. (American elm), *Acer rubrum* L. (red maple), *Betula alleghaniensis* Britton (yellow birch), *Thuja occidentalis* L. (northern white cedar), *Larix laricina* (Du Roi) K. Koch (tamarack), and *Picea mariana* (Mill) Britton, Sterns & Poggenb (black spruce, MNDNR, 2003). Although advance regeneration of tree species that are not EAB hosts is presently low in *F. nigra* wetland forests (Palik et al., 2011), the potential for one or more non-EAB-host tree species to replace *F. nigra* has not been adequately explored and silvicultural approaches for facilitating this replacement have not been investigated.

Silvicultural strategies such as artificial regeneration and overstory treatments have been suggested to restore species impacted by introduced disturbance agents (Dix et al., 2010). Overstory treatments can greatly enhance the potential for both natural and artificial regeneration success (Smith et al., 1996) For example, clearcuts may aid the establishment of shade-intolerant species, while group selection or shelterwood harvests can be used to make more subtle adjustments to the amount of light that reaches the forest floor, as well as to ameliorate changes in site hydrology (Slesak et al., 2014) and microclimate effects (Smith et al., 1996). Although experience with artificial regeneration in wetland forests has been limited to date, artificial regeneration combined with canopy treatment increased the recruitment of associated tree species in *Salix nigra* Marshall (black willow) wetland forests, with species selection exerting a greater influence on regeneration success than canopy treatment type (Dulohery et al., 2000).

The design of strategies to mitigate the effects of EAB-induced mortality on *F. nigra* ecosystems must take into account the uncertainties associated with climate change (Pedlar et al., 2012). If global emission increases continue on their current path (Pryor et al., 2014; Walsh et al., 2014), temperatures in northern Minnesota could rise by as much as 2.7^{o}C during the next half-century (Pryor et al., 2014), causing suitable climate locales for many tree species to shift 400-500 km NNE (Galatowitsch et al., 2009). Despite a projected slight increase in spring precipitation (Pryor et al., 2014), decreased summer rainfall (Pryor et al., 2014) and higher evapotranspiration rates would likely reduce wetland water budgets during the summer growing season (Galatowitsch et al., 2009), potentially benefitting less flood-tolerant *F. nigra*-associated tree species (Palik et al., 2011).

The predicted northeastward shift in suitable habitat in response to climate change (Galatowitsch et al., 2009) suggests that assisted range expansion of wetland tree species should be explored as a means of sustaining ecosystem functions over the longer term (Pedlar et al., 2012). Unlike assisted migration, which proposes rescuing non-native species from climate change by artificially moving them large distances, forestry-related assisted range expansion involves the northerly relocation of tree species to or within a few hundred kilometers of their current range limits (Pedlar et al., 2012). As such, it represents a potential tool for sustaining ecosystem function in imperiled forests and increasing forest resilience to future climate change (Pedlar et al., 2012). In terms of *F. nigra* forests, assisted range expansion could both extend the potential pool of available

tree species for maintaining post-EAB forest cover and promote tree species diversity to reduce risk from climate change and other forest threats (Pretzsch, 2005).

With these considerations in mind, we used an operational-scale field experiment in *F. nigra* wetlands to examine the survival of spring and fall plantings of 12 alternative tree species in response to four canopy treatments: uncut forest (control); girdling of all *F. nigra* ≥ 6 cm. diameter at breast height to emulate EAB-induced mortality; group selection (0.04 ha gaps covering 20% of plot); and clearcutting (1.6 ha patches). We used both spring and fall plantings to assess the effects of extensive spring ponding on seedling establishment. Our objectives were to determine: (1) the survival response of planted seedlings to canopy manipulations and emulated EAB-induced mortality, and (2) the most promising combination of species, overstory treatment, and planting season to inform diversification strategies.

2 Materials and Methods

2.1 Study sites and overstory treatments

We investigated the survival of potential *F. nigra*-replacement species using an operational-scale field experiment set in *F. nigra* wetlands in the Chippewa National Forest in northern Minnesota, USA (Figure 1). The climate is continental, with 1981-2010 high temperatures averaging -8.9 and 25.4°C in January and July, respectively (PRISM Climate Group, 2015). Mean precipitation for the same period was 742 mm yr^{-1}, with the majority of precipitation occurring from May through September. Plant communities at the sites are classified as WFn55 (northern wet *Fraxinus* swamp) grading

into WFn64 (northern very wet *Fraxinus* swamp), based on Minnesota native plant community classification (MNDNR, 2003). Soil texture varies from loam and sandy loam derived from glacio-fluvial or lacustrine parent materials to clay and silty clay derived from glacio-lacustrine material overlain by approximately 30 cm of muck (Slesak et al., 2014). Study site hydrology is strongly influenced by a confining clay layer, which coupled with flat topography, results in poor drainage (Slesak et al., 2014). Ponding occurs in the early part of the May to September growing season, with water tables typically declining below the ground surface by mid-July (Slesak et al., 2014). Water table fluctuations are largely dependent on precipitation (particularly snowmelt) and evapotranspiration, with only a very low absolute amount of shallow subsurface flow occurring (Slesak et al., 2014).

We divided the study area into eight experimental blocks based on preliminary observations of site moisture, proximity, and stand history. Most stands in blocks 1-6 were predominantly even-aged, whereas blocks 7 and 8 had multi-aged structures (A.W. D'Amato and M. Reinikainen, *unpublished data*). Before treatment, basal area for trees > 10.0 cm in diameter averaged 20.7 ± 2.2 m^2 ha^{-1} and mean tree density was 477 ± 50.6 trees ha^{-1}. The predominant overstory species was *F. nigra*, which comprised 91% of basal area, with minor components of *U. americana*, *Tilia americana* L. (American basswood), *Abies balsamea* (L.) Mill (balsam fir), *Populus tremuloides* Michx. (quaking aspen), and *Quercus macrocarpa* Michx. (bur oak).

Within each block, four 1.62 ha (radius 71.8m) circular plots were established, one of which was left as uncut forest to serve as a control, whereas each of the others

received one of three treatments. To emulate EAB-induced tree mortality, which research suggests may not occur for several years after infestation depending on tree carbohydrate reserves (Knight et al., 2010), a girdling treatment was applied to all *F. nigra* ≥ 6 cm DBH. A group selection treatment, consisting of eight 0.04 ha (400m^2) circular gaps, totaling a cleared area of approximately 20% of the 1.62 ha plot, was installed to test the potential for promoting regeneration through partial overstory removal prior to EAB invasion while limiting the water table rise associated with clearcutting (Erdmann et al., 1987). A clearcut treatment, involving the removal of all trees, was installed to evaluate the effects of preemptive salvage logging. All treatments were implemented in late winter 2012 under frozen ground conditions.

2.2 Artificial regeneration

We investigated the potential success of the following ten co-occurring tree species native to *F. nigra* forests in northern Minnesota: *B. alleghaniensis*, *Populus balsamifera* L. (balsam poplar), *L. laricina*, *Populus deltoides* W. Bartram ex Marshall (eastern cottonwood), *P. tremuloides*, *T. occidentalis*, *Picea mariana* (Mill) Britton (black spruce), *Acer rubrum* L. (red maple), *and U. americana* (MNDNR, 2003). In addition, we investigated two species with generally more southerly ranges: *Celtis occidentalis* L. (hackberry), of which isolated populations presently occur in the study area, and *Quercus bicolor* Willd. (swamp white oak), whose northern range limit lies approximately 100 mi SW of the study sites (Prasad et al., 2007) and that, like *F. nigra*, occurs as a dominant species in wetland forests in the northerly parts of its range. Finally,

to test its ability to survive local site conditions, we included *Fraxinus mandshurica* Rupr. (Manchurian ash), an EAB-resistant East Asian species closely related phylogenetically to *F. nigra* (Whitehill et al., 2010). *Fraxinus mandshurica* was included at the suggestion of USFS resource managers and members of local Native American tribes, who rely on *F. nigra* for their traditional basketry (personal communication, A.W. D'Amato), as well as to inform ongoing efforts to hybridize Asian and North American *Fraxinus* spp. to produce EAB-resistant cultivars (Koch et al., 2012).

Seedlings of species other than *Q. bicolor, P. balsamifera, F. mandshurica,* and *U. americana* were planted both prior to winter harvesting in fall 2011 (late August to late September) and after harvesting in spring 2012 (May to mid-June), so as to compare the effects of planting season. Seedlings were planted before harvesting with the assumption of sufficient snowpack to protect them from mechanical damage during the harvest treatments. Due to logistical constraints, fall plantings of *Q. bicolor, P. balsamifera,* and *F. mandshurica* were delayed until after harvesting in 2012, whereas *U. americana* was planted in spring 2012 only. Containerized seedlings included fall-planted *A. rubrum*, as well as *B. alleghaniensis, C. occidentalis*, *L. laricina*, *P. mariana, P. balsamifera, P. tremuloides,* and *T. occidentalis*: whereas bare-root stock seedlings included spring-planted *A. rubrum*, *F. mandshurica*, *P. deltoides*, and *Q. bicolor* (Table 1). *Ulmus americana* seedlings came from stock bred for tolerance to Dutch elm disease (*Ophiostoma novo-ulmi* Brasier) through crossing local seed sources from the Chippewa National Forest with the "Valley Forge" cultivar of *U. americana,* which exhibits proven tolerance to the disease (Townsend et al., 2005). Because similarly sized stock was

unavailable, *U. americana* seedlings were considerably larger in mean basal diameter, stem length and container size than seedlings of other species (Table 1).

Within each of the 1.62 ha treatment plots, we established six 0.04 ha ($400m^2$) subplots to serve as planting areas. In the group selection treatments, we centered four planting subplots within canopy gaps and dispersed two of them beneath undisturbed canopy. Using a planting bar (Smith et al., 1996), we planted eight rows of seedlings on the western half of each 0.04 ha subplot. The positions of species within rows were randomly allocated to planting locations within a planting frame, with 1.25m spacing between seedlings within rows and 2.5 m separation between rows. Given the importance of microsites to seedling survival in lowland systems, we planted each seedling on the closest favorable microsite to the randomly allocated planting location, avoiding hollows to the fullest extent possible given site topography. Random planting positions were not used for two species, *U. americana* and *F. mandshurica*, which were always located at the end of planting rows due to their late availability. For each species that received both spring and fall plantings, a total of 1536 seedlings was planted, distributed as 48 seedlings per species per treatment plot and 8 seedlings per species per planting subplot. For *U. americana*, which was planted only in spring, a total of 768 seedlings were planted, with 24 seedlings per species per treatment plot and 4 seedlings per species per planting plot. We assessed seedling survival at the beginning (May or June) and end (September or October) of each growing season from fall 2012 through fall 2014. We also inspected seedlings for the presence or absence of browse damage in spring 2013.

2.3 Analytical methods

We examined seedling survival for the final census period (fall 2014) using mixed-effects logistic regression. We analyzed the experiment as a split-plot design, with species and season of planting nested within overstory treatments. Random effects included 0.4 ha planting subplots nested within 1.62 ha treatment plots and experimental blocks. We initially modeled overall survivorship, excluding *U. americana* from the model, due to lack of spring plantings. Fixed factors included species, treatment, season of planting, and first-order interactions; we did not test second-level interactions due to difficulty of interpretation. The species with lowest survivorship, *B. alleghaniensis*, served as the reference level for species; the control served as the reference level for overstory treatment. Due to the large number of species and complexity of the analysis, we created individual-species models to more thoroughly investigate within-species treatment and seasonal effects. Because our analysis of *U. americana* was restricted to individual-species models, this species was not formally compared with the other 11 species.

We used backwards elimination to build initial sets of models, except in cases of significant interactions but insignificant main effects. We used Akaike's information criterion (AIC) to compare model parsimony for a given response variable and assessed overall model performance by calculating the area under the receiver operator characteristic (ROC) curve. In the event of a significant interaction but insignificant main effect, we calculated AIC of the model without the main effect but later refit the model to aid interpretability. We considered models with $\Delta AIC \leq 2$ to have similar support

(Burnham and Anderson, 2003). We performed post-hoc tests of species means, using Sidak adjustments for multiple comparisons. Mixed-effect logistic regressions were performed with the xtmelogit command in Stata 12 (StataCorp, 2011).

We graphically examined trends in mortality between census periods, treatments, and species. We used the ltable command in Stata 12 (StataCorp, 2011) to construct life tables of biannual, fall and spring census data, starting in fall 2012 and continuing through fall 2014. Despite the delayed planting of *Q. bicolor, F. mandshurica,* and *P. balsamifera,* we used survival as of fall 2012 as the starting point for all species, with the caveat that more recent plantings entered the study period with less time to die.

3 Results

3.1 Overall survival

The model of seedling survival, as measured in fall 2014, included overstory treatment, species, season, species x treatment, and species x season. We present only the most parsimonious models due to the high number of candidate models and the low weight of evidence (Δ AIC>10) for alternatives. Random block and subplot effects were significant for all models in Wald χ^2 tests (data not shown). Block effects accounted for more random variation than within-treatment subplot effects.

The mean overall survival rate for all species for all treatments and planting seasons was 30.7% ± 0.3% (Table 2). Mean overall survival by species across treatments and seasons was highest for *Q. bicolor* (75.5% ± 1.1%), *U. americana* (74.8% ± 2.1%), *F. mandshurica* (73.3% ± 1.1%), and *C. occidentalis* (52.9% ± 1.3%). In contrast, mean

overall survival across treatments and seasons was lowest for *B. alleghaniensis* (3.9% ± 0.5%) and *P. tremuloides* (4.8% ± 0.5%).

3.2 Overstory treatment x species interactions

Survival varied significantly by treatment ($F=13.01$, $p<0.001$) and species ($F=129.6$, $p<0.001$). However, due to a significant species x treatment interaction ($F=13.84$, $p<0.001$), the rank order of species in terms of survival varied between treatments (Figure 2). Mean overall survival rates, adjusted for the effects of species and season, were generally comparable in the control (32.9% ± 0.7%), girdle (33.3% ± 0.7%), and group selection (34.5% ± 0.7%) treatments (Table 2). Among the top-surviving species, *U. americana* (93% ± 2.6%), *Q. bicolor* (83.2% ± 1.9%), and *C. occidentalis* (76.7% ± 2.2%) achieved their highest rates of survival in the controls. *Ulmus americana* and *Q. bicolor* also achieved survival rates above 75% in the girdle and group selection treatments. *Fraxinus mandshurica* showed highest survival in the girdle treatments (84.4% ± 1.8%), followed by the group selection (78.3% ± 2.1%), and the control (74.4% ± 2.2%) treatments.

Overall survival was significantly lower in the clearcuts (22.1% ± 0.6%, Table 2, Figure 2). Seedling survival rates were lowest in the clearcuts for a full two-thirds of the species planted: *U. americana* (31.8% ± 0.5%), *Q. bicolor* (68.2% ± 0.2%), *C. occidentalis* (17.3% ± 0.2%), *F. mandshurica* (56.5% ± 0.3%), *A. rubrum* (14.7% ± 0.2%), *P. mariana* (11.4% ± 1.6%), *T. occidentalis* (4.2% ± 0.1%), and *B. alleghaniensis* (0.3% ± 0.3%). Although *L. laricina* also did poorly in the clearcuts (8.1% ± 1.4%), it

had comparably low survival rates in the control (8.1% ± 1.4%) and girdle (7.3% ± 1.4%) treatments. In contrast, survival rates were lowest in the controls for shade-intolerant *P. balsamifera* (28.5% ± 2.3%), *P. deltoides* (5.3% ± 1.1%), and *P. tremuloides* (0.3% ± 0.3%), which survived better in the clearcuts. Survival of *P. balsamifera* (45% ± 2.5%) was highest in the group selection treatments.

3.3 Planting season x treatment and season x species interactions

Although planting season did not have a significant main effect on overall survival ($F=1.79$, $p=0.18$), it interacted significantly with treatment ($F=13.83$, $p<0.001$, Figure 3) and species ($F=60.4$, $p<0.001$, Figure 4). When controlling for species effects, spring plantings in the group selection treatment had significantly higher survival than in control, whereas the girdle treatment had intermediate survival. In contrast, the control, girdle, and group selection treatments were comparable for fall plantings. Mean survival in the clearcut was significantly lower in both spring and fall compared with other treatments (Figure 3). When *U. americana*, which was planted only in spring, was excluded from the multi-species regression model, overall survival was higher for fall than for spring plantings (33.7% ± 1.4% vs 28.7% ± 1.9%, respectively, Table 2).

In terms of individual species, planting season was a significant predictor of survival for all species planted in both spring and fall, with the exception of *C. occidentalis* and *P. deltoides* (Table 3). Survival rates were superior for fall than for spring-planted *F. mandshurica* (83.7% ± 1.7% vs. 62.7% ± 1.3%, respectively, Table 2). Fall survival rates were also higher than spring survival rates for *L. laricina*, (14.03% ±

1.3% vs 5.2% ± 0.8%, respectively), *P. balsamifera* (46.5% ± 2.5% vs. 25.4% ± 1.6%, respectively), and *Q. bicolor* (85.5% ± 1.3% vs 65.3% ± 1.7%, respectively), but were partially contingent on treatment due to significant interaction effects (Table 2). Survival rates of spring plantings were superior to those of fall plantings for *A. rubrum* (37.9% ± 1.7% vs 17.5% ± 1.4%, respectively), *P. mariana* (32.6% ± 0.8% vs 5.6% ± 1.7%, respectively), *B. alleghaniensis* (5.2% ± 0.8% vs 2.6% ± 0.5%, respectively), *T. occidentalis* (17.6% ± 1.4% vs. 7.2% ± 0.9%, respectively), and *P. tremuloides* (6.8% ± 0.9% vs 2.9% ± 0.6%, respectively) but only slightly better for *C. occidentalis* (54.8% ± 1.8% vs 51.0% ± 1.8%, respectively, Table 2).

3.4 Treatment x species x planting season interactions

For *P. balsamifera, Q. bicolor,* and *L. laricina,* there was a significant three-way interaction among species, treatment, and planting season (Table 3). Fall plantings of *Q. bicolor* and *L. laricina* had higher survival except in the clearcut treatment, whereas survival of spring-planted *P. balsamifera* was lower in the control and girdle treatments.

3.5 Trends and Patterns

Plots of mean survival by census period (Figure 5) illustrate that differences in survival among overstory treatments were evident by fall 2012 and remained consistent through the end of the observation period in fall 2014. In fall 2012, overall survival was lowest in the clearcuts but above 50% for all treatments. In contrast, survival in the

clearcuts had fallen steadily to under 20% by fall 2014, whereas non-clearcut treatments had fallen to an average of about 30%.

Some early patterns of individual species survival demonstrated similar consistency (Figure 6). As might be expected, fall 2012 seedling survival was highest for *F. mandshurica* (98.6% ± .03%), *Q. bicolor* (95.9% ± 0.5%), and *U. americana* (86.2% ± 1.7%), i.e., the three species for which fall plantings were delayed until immediately prior to the fall 2012 census. However, at the close of the study in fall 2014, survival rates remained above 70% for all three species. *Celtis occidentalis*, which had a fall 2012 survival rate of 73.0% ± 1.3%, was the only spring-planted species still above its median life expectancy in fall 2014 (52.9% ± 1.3%). As early as fall 2012, heavy mortality had reduced survival to below 50% for *A. rubrum* (49.2% ± 1.3%), *B. alleghaniensis* (33.6% ± 1.2%), and *P. tremuloides* (24.6% ± 1.1%), as well as for the three conifer species, *T. occidentalis* (47.2% ± 1.3%), *P. mariana* (38.8% ± 1.2%), *and L. laricina* (17.8% ± 1.0%). By the end of the observation period, all three conifer species had survival rates below 20%.

4 Discussion

4.1 Overstory treatments

With the exception of the three shade-intolerant species, i.e., *P. balsamifera, P. deltoides* and *P. tremuloides* (Niinemets and Valladares, 2006), clearcutting was the least-successful canopy treatment for promoting survival of the various species of planted seedlings, a finding that is consistent with Erdmann's (1987) observation that clearcutting

F. nigra forest may result in loss of tree regeneration due to rising water tables. In a companion study on our experimental sites, Slesak et al. (2014) found that clearcutting caused a significant rise in the water table and duration of ponding during subsequent growing seasons, which could subject seedlings to greater inundation, waterlogging, and hypoxic conditions. Given the high observed first-year seedling mortality rates across sites, ponding may exert a strong control on survival during seedling establishment but decline in importance thereafter. The early death of seedlings planted on microsites that become inundated due to *F. nigra* mortality, combined with greater seedling size over time, may also reduce demonstrated sensitivity to soil saturation in subsequent years (Jones and Sharitz, 1998).

The low survival rates of all but the shade-intolerant *Populus* spp. in the clearcut treatment also suggests that greater light availability had a negative influence on seedling survival, presumably through its effect on the degree of understory competition. Slesak et al. (2014) noted that the herbaceous understory in our experimental plots responded vigorously to clearcutting 2 years after treatment, a response we also observed in the third year. A study examining the effectiveness of a willow overstory on hardwood restoration similarly found that overstory removal was counterproductive to artificial tree regeneration, increasing microclimatic extremes, herbaceous layer cover, and seedling mortality (Dulohery et al., 2000). Wang et al. (2013) concluded that *F. mandshurica* growing in its native range faced heavy root competition from herbaceous species, particularly when grown without a forest overstory. Not only may the increased light availability from clearcutting indirectly interfere with seedling survival by increasing

competition from the herbaceous layer, but Royo and Carson (2006) suggested that clearcutting *F. nigra* swamps may result in a recalcitrant understory layer with long-term effects on the reestablishment of forest cover. Based on these findings, the regeneration response in *F. nigra* forests in the presence or absence (i.e., competition control) of a dense herbaceous layer should be examined in greater detail.

Control, group selection, and girdle treatments showed equivalent overall survival for the first several years after planting for the four top-surviving species, *Q. bicolor*, *F. mandshurica, U. americana,* and *C. occidentalis*. However, the long-term efficacy of growing replacement species under an intact *F. nigra* overstory, as in the control, is unknown. As seedlings mature, the negative impacts of shading in the control plots may replace facilitative effects during establishment (Callaway and Pugnaire, 2007; Dulohery et al., 2000). In the group selection treatment, we found simultaneously high survival of shade-tolerant species such as *C. occidentalis* and improved success of shade-intolerant *Populus* spp. and *L. laricina* compared with the control. If growth is light-limited, group selection could be effective at both promoting development and supporting a larger variety of species. In addition, water table response (shallower depth, longer duration of ponding) in the group selection treatment was negligible and very similar to the control (Slesak et al., 2014), suggesting that the residual overstory in the group selection may ameliorate the degree of inundation experienced by seedlings. Comparable survival in the girdle treatment suggests that planting immediately prior to EAB invasion could achieve a shelterwood effect, with seedlings initially benefitting from overstory microclimatic effects (Aussenac, 2000), but later released following the loss of the canopy (Smith et al.,

1996). However, a concurrent rise in the water table following girdling (Slesak et al. 2014) may offset any positive benefits of a shelterwood effect.

4.2 Species survival

Mortality rates were high in the first year of the study, with the majority of species having less than 50% survival in the growing season immediately after harvest. Mortality rates over the rest of the study declined, generally maintaining the relative species differences that were apparent by fall 2012. First-year seedling survival was likely impacted by a series of unusual climate events. Fall 2011 marked the onset of a moderate to severe drought, which persisted through 2012 and translated into below-average 2011-2012 snowfall (average Palmer Drought Severity Index = 2.63, National Climate Data Center, 2015). Reduced snow cover can subject the rooting zone to lower temperatures and dramatically increase vulnerability to frost heaving (Bergsten et al., 2001), visual evidence of which was reported by the field crew in fall 2012. Below-average snow cover may also have exposed seedlings in the clearcut and group selection treatments to logging damage, as 2011 fall plantings were installed prior to harvesting with the expectation of a protective snowpack, so that no additional provisions were assumed to be necessary for their protection. In addition, a record warming trend in March 2012 disrupted the dormancy period and resulted in a prolonged freeze-thaw cycle (National Climate Data Center, 2015). Finally, unusual flooding occurred when 12.7 cm of rain fell on the study area in a 24-hour period on 19-20 June 2012 (National Climate Data Center, 2015).

Quercus bicolor, F. mandshurica, and *P. balsamifera,* half of which were planted in the fall after harvest, and *U. americana*, which was planted only in the spring after harvest, entered the study period with higher survival. Nevertheless, survival rates for these species remained comparatively stable through subsequent measurement periods, suggesting inherently higher overall survival rates. The high survival rate of *U. americana* was comparable with that found in a previous study that examined experimental plantings of the species in *Fraxinus* forests in Ohio (Knight et al., 2012). *Ulmus americana*'s high survival rate may reflect both suitability to *F. nigra* forests and the large average size of seedlings in both studies (Knight et al., 2012). Large seedling size may confer an advantage in wetlands by elevating leaves above standing water (Knight et al., 2012), which may also explain, in part, the high survival rates of non-native *Q. bicolor* and *F. mandshurica* compared with naturally occurring species with smaller planting stock such as *B. alleghaniensis* and *T. occidentalis*. Similarly, root growth increases seedlings' ability to compete for soil resources, store carbohydrates (Smith et al., 1996), and escape damage from frost heaving (Goulet, 1995). Thus, *P. balsamifera,* which was smaller than lower-surviving *P. deltoides* in terms of pre-planting mean basal diameter and stem length, may have benefitted from superior root development due to its larger container size.

Our findings suggest *U. americana, Q. bicolor,* and *C. occidentalis* appear to hold promise as *F. nigra* replacement species in the ecosystems examined. *Ulmus americana* was common in the study ecosystems before the spread of Dutch elm disease (A.W. D'Amato and M. Reinikainen, unpublished data), and the availability of Dutch elm

disease-resistant cultivars makes its reintroduction feasible. The long-term ability of *Q. bicolor* and *C. occidentalis* to grow and naturally reproduce in *F. nigra* wetlands has not yet been tested, whereas *C. occidentalis* has shown low natural regeneration in standing water and may be growth limited on wet sites (Krajecek and Williams, 1990). However, *Q. bicolor* seedlings have previously demonstrated high survival and positive growth under open, flooded conditions (Kabrick et al., 2012). Furthermore, a predicted decrease in precipitation and shift in suitable habitat to the NNE with warming climate could make both species excellent candidates for assisted range expansion in the longer term (Williams and Dumroese, 2013). In the short term, these species might also serve as a "nurse crop" (Landhäusser et al., 2003), regulating water tables and microclimatic conditions until more suitable species can be established.

Given the relative success of *C. occidentalis* and *Q. bicolor*, which were respectively planted at or beyond the northern limits of their present ranges, assisted range expansion could improve the available species pool for maintaining long-term forest cover in post-EAB *F. nigra* wetlands (Pedlar et al., 2012). Because *Q. bicolor* occurs, like *F. nigra*, both as an associated species in mixed-hardwood forests and a dominant species in more northerly wetland forests (Snyder, 1992), its functional traits should be explored to determine if it might potentially fill *F. nigra*'s niche in very wet northern ecosystems. At present, an insufficient number of degree days for flowering success appears to define the northern range limit of *Q. bicolor* (Morin et al., 2007), as opposed to lack of physiological tolerance, suggesting that the species might become better suited to northern Great Lakes forests as the growing season lengthens with climate

change (Pryor et al., 2014). Future research might also explore whether there are other wetland-forest-dominant or co-dominant species with similar range distributions currently limited by phenology.

Populus balsamifera and *F. mandshurica* are more problematic. *Populus balsamifera*, a minor forest component on our study sites prior to treatment, achieved less than a 50% 3-year survival rate under the best combination of treatment and planting season. Moreover, even if the population of *P. balsamifera* could successfully be increased in the near-term, the species is predicted to suffer heavy declines in Minnesota as a result of climate change (Iverson et al., 2008). *Fraxinus mandshurica*, which more typically occurs on sites with well drained soils, had an impressively high rate of survival, possibly reflecting exposure to harsher winter conditions within much of its native range compared with our study area (Qian et al., 2003). However, we are not advocating for its assisted migration into North American *F. nigra* wetland forests, an intercontinental species introduction that could pose unknown and unacceptable risks such as the development of invasive behavior and other interactions with native species (Pedlar et al., 2012). Our results do, however, indicate that as part of a crossbreeding program to develop EAB-resistant *F. nigra*, pure *F. mandshurica* appears inherently tolerant of northern Minnesota growing conditions, although it may suffer winter dieback if not covered by an insulating layer of snow (A. D'Amato, personal observation).

Replacing *F. nigra* with *L. laricina*, a naturally occurring conifer species in northern Minnesota *F. nigra* forests (MNDNR 2003), has been suggested for the study areas (University of Minnesota Extension and MNDNR, 2011). However, the relative

success of angiosperm replacement species suggests *F. nigra* forests after EAB invasion could avoid the dramatic changes associated with conversion to a conifer-dominated forest. Such changes with conversion from one life-form to another have been observed in other North American forests affected by invasive insects (Ford et al., 2012).

4.3 Planting season

We found the season of planting can influence survival in combination with overstory management and/or species selection. Although fall plantings did not show higher survival in clearcuts and group selections, they resulted in significantly higher survival in controls. Although harvesting-related mechanical damage to 2011 fall-planted seedlings likely contributed to this result, fall plantings in general may face higher risk of frost heaving in harvest treatments than in closed forest due to reduced overstory cover and soil scarification (Goulet, 1995).

Although Hansen (1986) found that fall plantings of *P. deltoides* hybrids in Wisconsin resulted in higher mortality, which the author attributed to frost heaving, we found no significant difference between seasons when using standard *P. deltoides* stock on wetter, non-intensively managed sites. Among the conifer species, we found that fall-planted *L. laricina* had higher survival except in clearcuts, whereas *P. mariana* and *T. occidentalis* showed the opposite pattern. Takyi and Hillman (2000) reported similar survival between spring and fall plantings of *L. laricina* and *P. mariana* grown in clearcuts. Examining only seedlings in the clearcuts, we found no difference in survival for *L. laricina* between seasons but significantly lower survival of *P. mariana*. The

unusually low snowfall of winter 2011-2012 may have promoted desiccation in the evergreen *P. mariana* seedlings tested in this study (Christersson and von Fircks, 1988), while providing little protection from deer herbivory and machine traffic during harvesting. Operationally, we found that fall planting was more efficient due to improved accessibility with drier soil conditions.

5 Conclusions

Our results indicate that planting of tree species that are not EAB hosts, both with and without overstory harvest treatments, is a potentially viable management option for sustaining forest cover and ecosystem services in F. nigra wetlands threatened by EAB invasion. Although our results suggest that clearcutting, as is used with preemptive salvage logging, negatively impacted the survival of 9 of 12 species we tested, unanticipated mechanical damage to seedlings during harvesting may have worsened survival in clearcuts and group selections. Nonetheless, control, group selection, and girdling treatments (which are emulative of planting just prior to EAB infestation) showed roughly equivalent seedling survival responses for the first several years. By maintaining overstory cover while locally increasing understory light availability, group selection could be effective in promoting seedling development, while supporting a wider variety of tree species and maintaining hydrologic conditions similar to the uncut forest and favorable to seedling establishment. Species selection will be critical to the success of any future planting effort, with conifer and shade-intolerant hardwood species showing generally low survival rates. The more robust seedling stock of high-surviving species

such as *U. americana, Q. bicolor* and *F. mandshurica* suggests that future research and planting efforts should prioritize stock quality. Although damage during winter harvesting may have reduced the overall effectiveness of fall plantings, our results nevertheless suggest that planting season should be determined based on species and overstory treatment type to assure the greatest chance of seedling survival. Further research is needed to predict how factors such as herbaceous plant communities and herbivore activity may interact with overstory management and artificial regeneration. In addition to survival, growth rates and fecundity of replacement species over longer time periods with different management options need to be evaluated.

References

Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Ann. For. Sci. 57, 287–301 http://dx/doi.org/10.1051/forest:2000119.

Benedict, M.A., Frelich, L.E., 2008. Site factors affecting black ash ring growth in northern Minnesota. For. Ecol. Manag. 255, 3489–3493. http://dx/doi.org/10.1016/j.foreco.2008.02.029.

Bergsten, U., Goulet, F., Lundmark, T., Löfvenius, M.O., 2001. Frost heaving in a boreal soil in relation to soil scarification and snow cover. Can. J. For. Res. 31, 1084–1092. http://dx/doi.org/10.1139/x01-042.

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Callaway, R.M., Pugnaire, F.I., 2007. Facilitation in plant communities, in: Pugnaire, F.I., Valladeres, F. (Eds.), Functional Plant Ecology. CRC Press, Boca Raton, FL,pp. 435–453.

Christersson, L., von Fircks, H.A., 1988. Injuries to conifer seedlings caused by simulated summer frost and winter desiccation. Silva Fenica 22, 195–201.

Cohen, J.G., Kost, M.A., Slaughter, B.S., Albert, D.A., 2014. A Field Guide to the Natural Communities of Michigan. Michigan State University Press, East Lansing, MI.

Dix, M.E., Buford, M., Slavicek, J.M., Solomon, A.M., Conrad, S.G., 2010. Invasive species and disturbances: Current and future roles of Forest Service research and development, in: A Dynamic Invasive Species Research Vision: Opportunities and Priorities 2009-29. pp. 91–102. https://www.fs.fed.us/research/docs/invasive-species/wo_gtr79_83/ wo_ gtr79_ 83_091.pdf (accessed 12.2.2014).

Dulohery, C.J., Kolka, R.K., McKevlin, M.R., 2000. Effects of a willow overstory on planted seedlings in a bottomland restoration. Ecol. Eng. 15, S57–S56. http://dx/doi.org/10.1016/S0925-8574(99)00072-5.

Epstein, E.J., Judziewicz, E.J., Spencer, E.A., 2002. Northern Hardwood Swamp, in: Wisconsin Natural Community Abstracts. Department of Natural Resources, Bureau of Endangered Resources, Madison, WI.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115.

Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., Vose, J.M., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos 121, 523–536. http://dx/doi.org/10.1111/j.1600-0706.2011.19622.x.

Galatowitsch, S., Frelich, L., Phillips-Mao, L., 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol. Conserv. 142, 2012–2022. http://dx/doi.org/10.1016/j.biocon.2009.03.030.

Goulet, F., 1995. Frost heaving of forest tree seedlings: A review. New For. 9, 67–94. http://dx/doi.org/10.1007/BF00028927.

Gucker, C.L., 2005. *Fraxinus nigra*. Fire Eff. Syst. http://www.fs.fed.us/database/feis (accessed 6.10.15).
Hansen, E.A., 1986. Planting date affects survival and height growth of hybrid poplar. For. Chron. 62, 164–169. http://dx/doi.org/10.5558/tfc62164-3.
Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts and management. Annu. Rev. Entomol. 59, 13–30. http://dx/doi.org/10.1146/annurev-ento-011613-162051.
Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manag., Forest landscape modeling - Approaches and applications 254, 390–406. http://dx/doi.org/10.1016/j.foreco.2007.07.023.
Jones, R.H., Sharitz, R.R., 1998. Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. J. Ecol. 86,574–587. http://dx/doi.org/10.1046/j.1365-2745.1998.00287.x.
Kabrick, J.M., Dey, D.C., Van Sambeek, J.W., Coggeshall, M.V., Jacobs, D.F., 2012. Quantifying flooding effects on hardwood seedling survival and growth for bottomland restoration. New For. 43, 695–710. http://dx/doi.org/10:1007/s11056-012-9331-y.
Kashian, D.M., Witter, J.A., 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. For. Ecol. Manag. 261, 480–488. http://dx/doi.org/10.1016/j.foreco.2010.10.033.
Knight, K.S., Herms, D.A., Cardina, J., Long, R., Rebbeck, J., Gandhi, K.J., Smith, A., Klooster, W.S., Herms, C.P., Royo, A.A., 2010. Emerald ash borer aftermath forests: the dynamics of ash mortality and the responses of other plant species: Notes, in: Michler, C.H., Ginzel, M.D. (Eds.), Proceedings of Symposium on Ash in North America. USDA Forest Service, Northern Research Station, Newton Square, PA, Gen. Tech. Rep. NRS P-72. p. 11.
Knight, K.S., Slavicek, J.M., Kappler, R., Pisarczyk, E., Wiggin, B., Menard, K., 2012. Using Dutch elm disease-tolerant elm to restore floodplains impacted by emerald ash borer, in: Proceedings of the 4th International Workshop on Genetics of Host-Parasite Interactions in Forestry. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, Gen. Tech. Rep. PSW-GTR-240, pp. 317–323.
Koch, J.L., Carey, D.W., Knight, K.S., Poland, T.M., Herms, D.A., Mason, M.E., 2012. Breeding strategies for the development of emerald ash borer-resistant North American ash, in: Proceedings of the 4th International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. pp. 235–239.
Krajecek, J.E., Williams, R.D., 1990. *Celtis occidentalis* L.: Hackberry, in: Burns, R.M., Honkala, B.H., tech. coord. (Eds.), Silvics of North America: Volume 2 Hardwoods, Agricultural Handbook 654. USDA Forest Service, Washington, D.C., p. 877.
Landhäusser, S.M., Lieffers, V.J., Silins, U., 2003. Utilizing pioneer species as a hydrological nurse crop to lower water table for reforestation of poorly drained boreal

sites. Ann. For. Sci. 60, 741–748. http://dx/doi.org/10.1051/forest:2003068
Lenhart, C., Brooks, K., Davidson, M., Slesak, R., D'Amato, A., 2012. Hydrolic source characterization of black ash wetlands: Implications for EAB response. Presented at the AWRA Summer Specialty Conference on Riparian Ecosystems, Denver, CO, June 27-29. 6 pp.
MNDNR, 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, MN.
Morin, X., Augspurger, C., Chuine, I., 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology 88, 2280. http://dx/doi.org/10.1111/j.1365-2699.2011.02659.x.
National Climate Data Center, 2015. Minnesota Climate Division 2. http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers (accessed 5.28.15).
Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. http://dx/doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. For. Ecol. Manag. 269, 26–30. http://dx/doi.org/10.1016/j.foreco.2011.12.020.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2011. *Fraxinus nigra* (black ash) dieback in Minnesota: Regional variation and potential contributing factors. For. Ecol. Manag. 261, 128–135. http://dx/doi.org/10.1016/j.foreco.2005.03.013.
Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. BioScience 62, 835–842. http://dx/doi.org/10.1525/bio.2012.62.9.10.
Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. For. 104, 118–124.
Prasad, A.M., Iverson, L.R., Matthews, S., Peters, M., 2007. Change Tree Atlas (A Spatial Database of 134 Tree Species of the Eastern USA). USDA Forest Service, Northern Research Station, Newton Square, PA. http://www.nrs.fs.fed.us/atlas/tree (accessed 3.3.15).
Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots, in: Forest Diversity and Function, Ecological Studies. Springer: Verlag, Berlin-Heidelberg, pp. 41–64.
PRISM Climate Group, 2015. PRISM climate data: Recent years (Jan 1981-June 2014). Northwest Alliance Comput. Sci. Eng. http://www.prism.oregonstate.edu/recent/ (accessed 1.11.15).
Pryor, S.C., Scavia, D., Downer, C., Gaden, M., Iverson, L.R., Nordstrom, R., Patz, J., Robertson, G.P., 2014. Ch. 18: Midwest, in: Melillo, J.., Richmond, T.C., Yohe, G.W. (Eds.), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, pp. 418–440.

Pugh, S.A., Liebhold, A.M., Morin, R.S., 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can. J. For. Res. 41, 2165–2175. http://dx/doi.org/10.1139/x11-138.

Qian, H., Yuan, X.-Y., Chou, Y.-L., 2003. Forest vegetation of northeast China, in: Kolbeck, J., Srutek, M., Box, E.O., eds., Forest Vegetation of Northeast Asia. Springer, Dordrecht, The Netherlands, pp. 181–230.

Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. http://dx/doi.org/10.1139/x06-025.

Scott, G.A.J., 1995. Canada's Vegetation: A World Perspective. McGill-Queen's Press, Montreal, Quebec.

Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx/doi.org/10.1139/cjfr-2014-0111.

Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1996. The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley and Sons, New York, NY.

Snyder, S.A., 1992. *Quercus bicolor*. Fire Eff. Inf. Syst. http://www.fs.fed.us/database/feis (accessed 5.28.15).

StataCorp, 2011. Stata, Stata Statistical Software: Release 12. StataCorp L.P., College Station, TX.

Takyi, S.K., Hillman, G.R., 2000. Growth of coniferous seedlings on a drained and mounded peatland in central Alberta. North. J. Appl. For. 17, 71–79.

Telander, A.C., Slesak, R.A., D'Amato, A.W., Palik, B.J., Brooks, K.N., Lenhart, C.F., 2015. Sap flow of black ash in wetland forests of northern Minnesota, USA: Hydrologic implications of tree mortality due to emerald ash borer. Agric. For. Meteorol. 206, 4–11. http://dx/doi.org/10.1016/j.agrformet.2015.02.019.

Townsend, A.M., Bentz, S.E., Douglass, L.W., 2005. Evaluation of 19 American elm clones for tolerance to Dutch elm disease. J. Environ. Hortic. 23, 21–24.

University of Minnesota Extension and MNDNR, 2011. Ash Management Guidelines for Private Forest Landowners. University of Minnesota Extension Service, St. Paul. MN.

Walsh, J.D., Wuebbles, D., Hayhoe, K., Kossin, J., Kunkel, K., Stephens, G., Thorne, P., Vose, R.P., Wehner, M., Willis, J., 2014. Chapter 2: Our Changing Climate, in: Melillo, J.., Richmond, T.C., Yohe, G.W. (Eds.), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, pp. 19–67.

Wang, J., Wu, L., Zhao, X., Fan, J., Zhang, C., Von Gadow, K., 2013. Influence of ground flora on *Fraxinus mandshurica* seedling growth on abandoned land and beneath forest canopy. Eur. J. For. Res. 132, 313–324. http://dx/doi.org/10.1007/s10342-012-0676-8.

Whitehill, J.G.A., Herms, D.A., Bonello, P., 2010. Exploring the molecular and

biochemical basis of ash resistance to emerald ash borer, in: Proceedings of the Symposium on Ash in North America. USDA Forest Service, Northern Research Station, Newton Square, PA, Gen. Tech. Rep. NRS-P-72, pp. 9–23.
Williams, M.I., Dumroese, R.K., 2013. Preparing for climate change: forestry and assisted migration. J. For. 111, 287–297. http://dx/doi.org/10.5849/jof.13-016.

Table 1. Mean basal diameter (± standard error S.E.)), mean stem length ±S.E., and stock type at planting for seedlings of 12 potential *Fraxinus nigra* replacement tree species, based on a random sample of 100 seedlings per species.

Species	Mean basal diameter (mm)	Mean stem length (cm)	Stock type
Acer rubrum	4.7 (0.17)	22.1 (1.13)	Container (90 cm^3)
Betula alleghaniensis	3.4 (0.55)	21.8 (0.63)	Container (90 cm^3)
Celtis occidentalis	5.1 (0.14)	44.7 (1.37)	Container (336 cm^3)
Fraxinus mandshurica	9.1 (0.26)	78.7 (1.28)	Bareroot (3+0)
Larix laricina	3.9 (0.09)	28.5 (0.86)	Container (60 cm^3)
Picea mariana	3.9 (0.08)	42.4 (0.66)	Container (90 cm^3)
Populus balsamifera	3.5 (0.08)	29.8 (0.73)	Container (164 cm^3)
Populus deltoides	4.5 (0.11)	38.6 (1.18)	Bareroot (1+0)
Populus tremuloides	3.1 (0.05)	21.0 (0.38)	Container (90 cm^3)
Quercus bicolor	4.7 (0.13)	25.4 (0.64)	Bareroot (1+0)
Thuja occidentalis	2.6 (0.77)	23.2 (0.37)	Container (60 cm^3)
Ulmus americana	10.3 (0.50)	95.4 (0.98)	Container (1890 cm^3)

Note: Values in parentheses under stock type correspond to container volume for containerized seedlings and number of years spent in nursery and transplant beds for bare-root stock. Measurements were taken prior to planting for all species but *U. americana,* which was measured just after planting.

Table 2. Mean survival (± standard error (S.E.)) by treatment and planting season with overall averages for seedlings of 12 tree species

		Treatment				Planting season	
Species	Overall	Clearcut	Control	Girdle	Group	Fall	Spring
ACRU	27.8d (1.1)	14.7a (1.8)	33.3b (2.4)	29.6b (2.3)	33.5b (2.4)	17.5a (1.4)	37.9b (1.7)
BEAL	3.9a (0.5)	0.3a (0.3)	3.9b (1.0)	4.9b (1.1)	6.5b (1.3)	2.6a (0.6)	5.2b (0.8)
CEOC	52.9f (1.3)	17.3a (1.9)	76.7d (2.2)	66.1c (2.4)	51.6b (2.5)	51.0a (1.8)	54.8a (1.8)
FRMA	73.3g (1.1)	56.5a (2.5)	74.4b (2.2)	84.4c (1.8)	78.3bc (2.1)	83.7b (1.3)	62.7a (1.7)
LALA	9.6b (0.8)	8.1a (1.4)	8.1a (1.4)	7.3a (1.3)	14.8b (1.8)	14.0b (1.3)	5.2a (0.8)
PIMA	19.1c (1.0)	11.4a (1.6)	17.4ab (1.9)	24.9c (2.2)	22.7bc (2.1)	5.6a (0.8)	32.6b (1.7)
POBA	36.0e (1.2)	39.3bc (2.5)	28.5a (2.3)	31.2ab (2.4)	45c (2.5)	46.5b (1.8)	25.4a (1.6)
PODE	11.0b (0.7)	11.6b (1.5)	5.3a (1.1)	10.9b (1.5)	16b (1.7)	9.6a (1.0)	12.2a (1.1)
POTR	4.8a (0.5)	7.6b (1.4)	0.3a (0.3)	3.2a (0.9)	8.4b (1.4)	2.9a (0.6)	6.8b (0.9)
QUBI	75.5g (1.1)	68.2a (2.4)	83.2b (1.9)	74.4a (2.2)	76.5ab (2.1)	85.5b (1.3)	65.3a (1.7)
THOC	12.4b (0.8)	4.2a (1.0)	16.1b (1.9)	15.5b (1.8)	13.8b (1.8)	7.2a (0.9)	17.6b (1.4)
ULAM*	74.8 (2.1)	31.8a (4.5)	93b (2.6)	91.3b (2.8)	87b (3.4)	74.8 (2.1)	N/A
Total	30.7 (0.3)	22.1a (0.6)	32.9b (0.7)	33.3b (0.7)	34.5b (0.7)	32.0a (0.5)	29.4a (0.5)

Note: Overall=species survival for all treatments and seasons. Lowercase letters adjacent to means represent pairwise comparisons of treatments and seasons based on individual-species models, adjusted for interactions when present. Levels not connected by the same lowercase letter are significantly different ($p<0.05$). Species are abbreviated as follows: ACRU=*Acer rubrum,* BEAL=*Betula alleghaniensis,* CEOC=*Celtis occidentalis,* FRMA=*Fraxinus mandshurica,* LALA=*Larix laricina,* PIMA=*Picea mariana,* POBA=*Populus balsamifera,* PODE=*Populus deltoides,* POTR=*Populus tremuloides,* QUBI=*Quercus bicolor,* THOC=*Thuja occidentalis,* ULAM= *Ulmus americana.* For ULAM, there was no fall planting, with a bivariate model only. **Mean ± S.E. includes ULAM, pairwise comparison excludes ULAM. NA=not available.

Table 3. Summary of results for best-supported models of individual-species survival.

Model	Treatment	Season	Treatment x season	F statistic	*p* statistic	ROC
ACRU	<0.001	<0.001	N.S.	30.95	<0.001	0.76
BEAL	0.007	0.009	N.S.	4.69	<0.001	0.81
CEOC	<0.001	N.S.	N.S.	85.5	<0.001	0.76
FRMA	<0.001	<0.001	N.S.	41.2	<0.001	0.77
LALA	0.002	<0.001	<0.001	11.81	<0.001	0.76
PIMA	<0.001	<0.001	N.S.	42.73	<0.001	0.81
POBA	<0.001	<0.001	<0.001	18.99	<0.001	0.74
PODE	<0.001	N.S.	N.S.	8.69	<0.001	0.74
POTR	<0.001	<0.001	N.S.	8.44	<0.001	0.87
QUBI	<0.001	<0.001	<0.001	14.84	<0.001	0.74
THOC	0.012	<0.001	N.S.	16.61	<0.001	0.77
ULAM	<0.001	N/A	N.S.	30.61	<0.001	0.89

Note: Potential model terms included treatment, season, and the treatment x season interaction. Significant terms have corresponding p-values, whereasn non-significant terms are designated “N.S.” Overall model F-statistics, p-values, and area under the receiver operating curve (ROC) are also provided. Species abbreviations are provided in Table 2. N/A=not available.

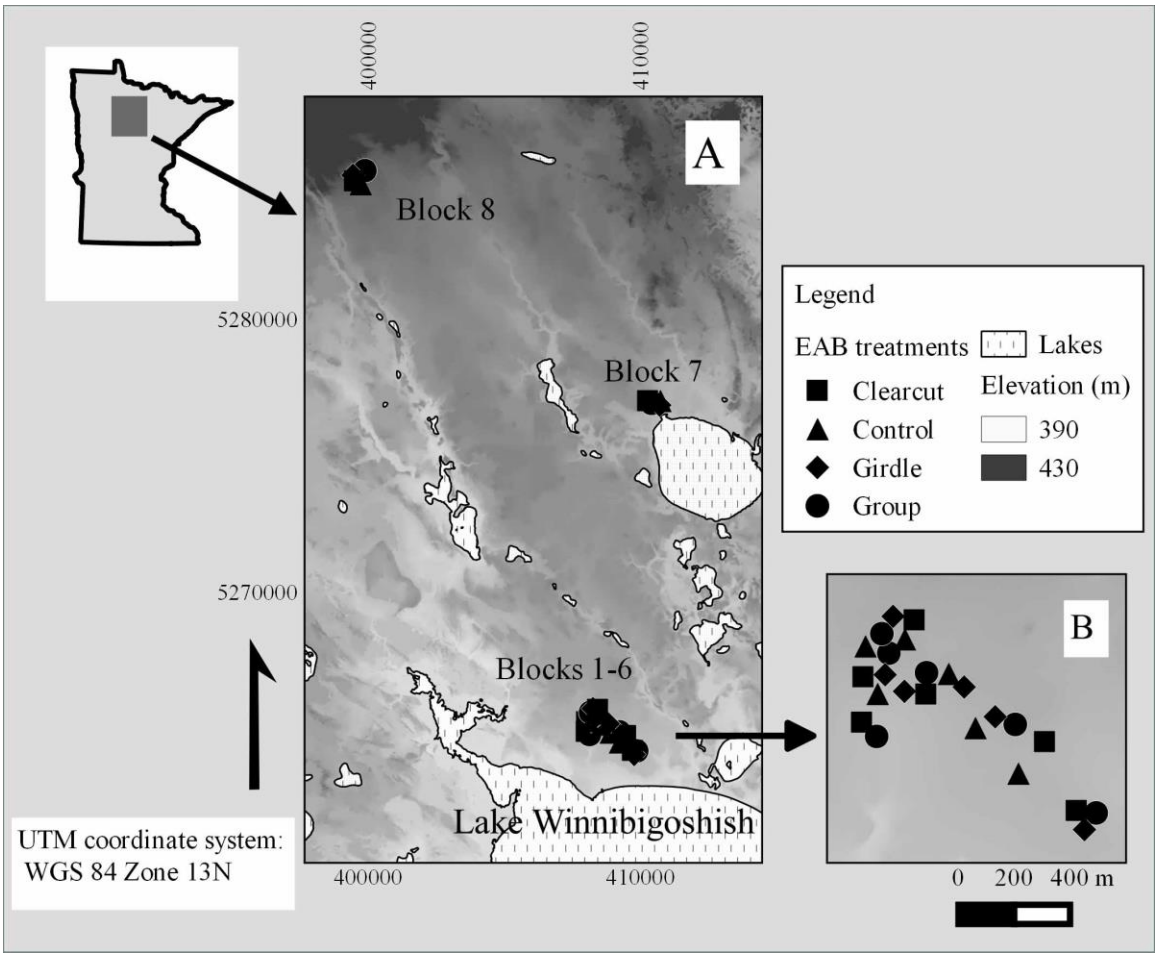

Figure 1. A) Map showing location of study sites near and within the Lake Winnibigoshish watershed in Minnesota, USA. B) Illustration of approximate layout of overstory treatment plots in Blocks 1-6, with treatments replicated once per block. Symbols not to scale. Blocks 7 and 8 similar in layout to blocks 1-6.

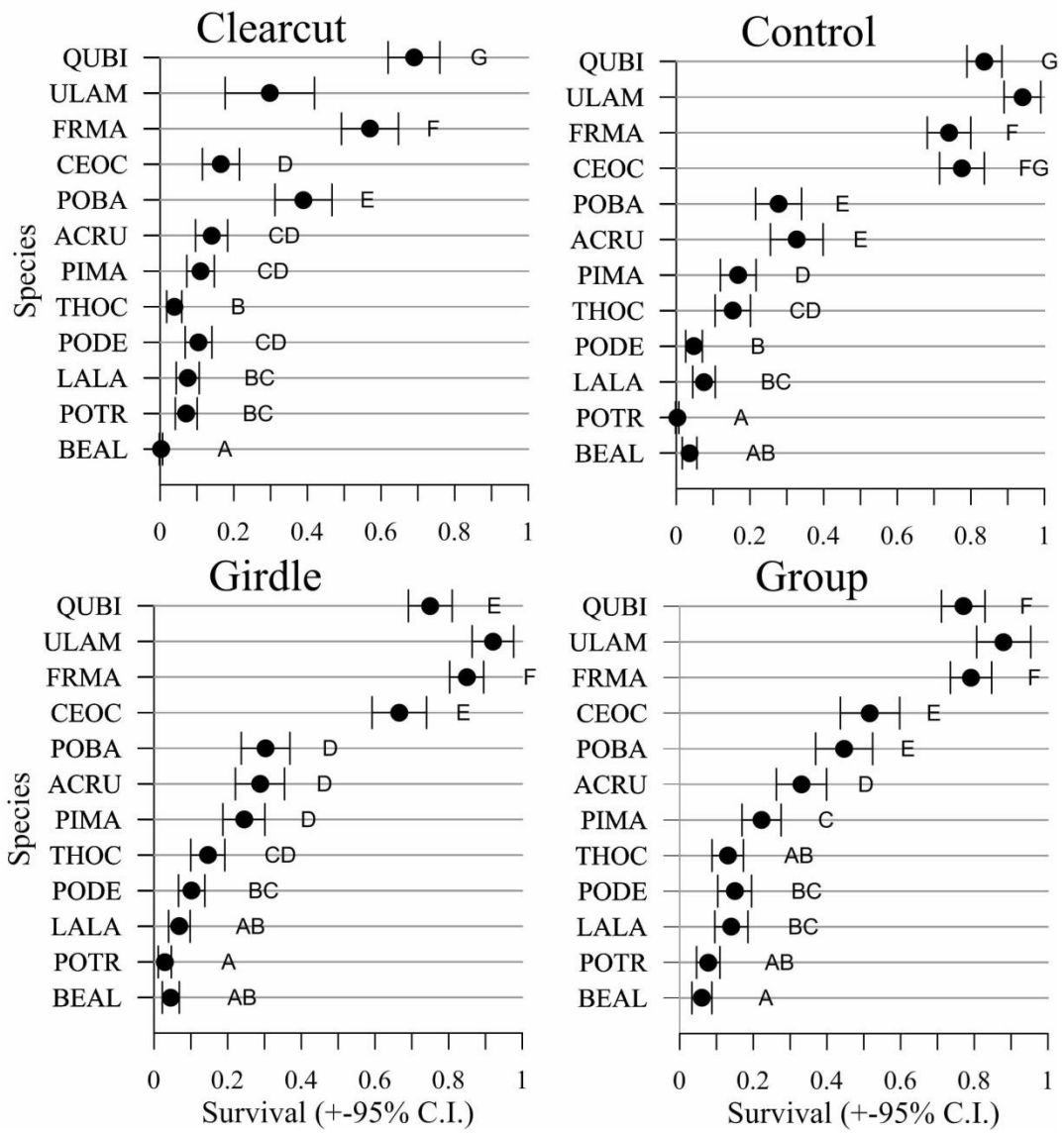

Figure 2. Interaction plot of the survival of seedlings of 12 species planted under clearcut, control, girdle and group selection treatments (mean $\pm$ 95% confidence interval (C.I.)), as assessed in fall 2014. Uppercase letters represent pairwise comparisons of species performed separately for each treatment; species not connected by the same letter are significantly different ($p<0.05$). See Table 2 for species abbreviations.

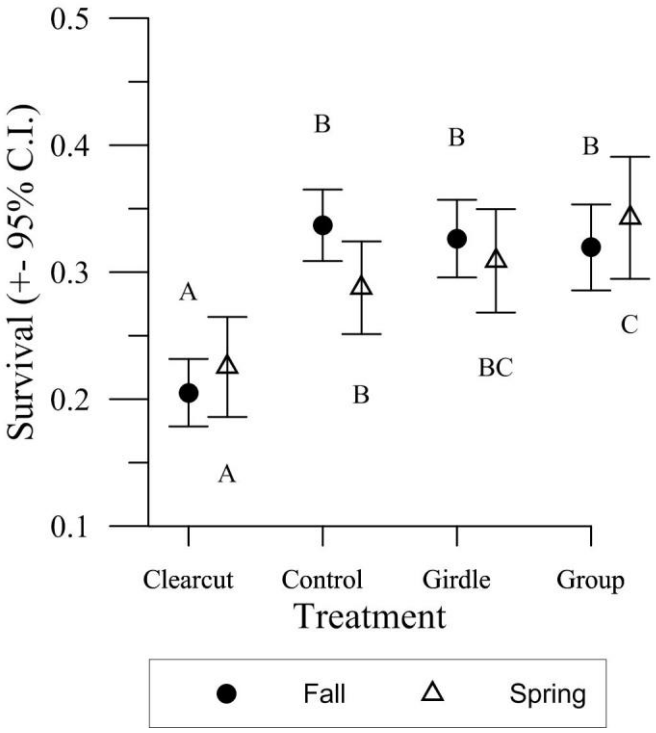

Figure 3. Interaction plot of the influence of overstory treatment and season on planting of average seedling survival (mean ± 95% confidence interval (CI)), as of fall 2014. Uppercase letters represent pairwise comparisons of treatments performed separately for each season. Treatments not connected by the same letter are significantly different ($p<0.05$). See Table 2 for species abbreviations.

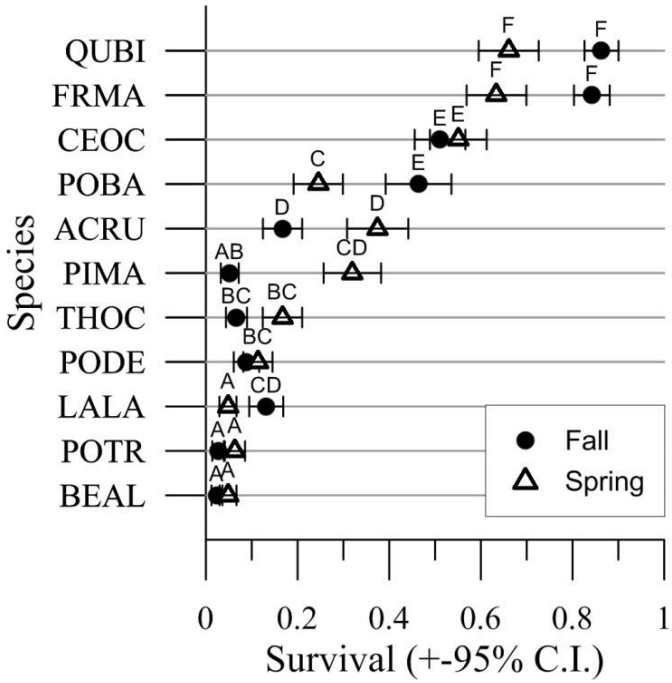

Figure 4. Interaction plot of the survival of spring and fall plantings of seedlings of 12 tree species (mean ± 95% confidence interval (C.I.), as assessed in fall 2014. Uppercase letters represent pairwise comparisons of species performed separately for each season. Species not connected by the same letter are significantly different ($p<0.05$). See Table 2 for species abbreviations.

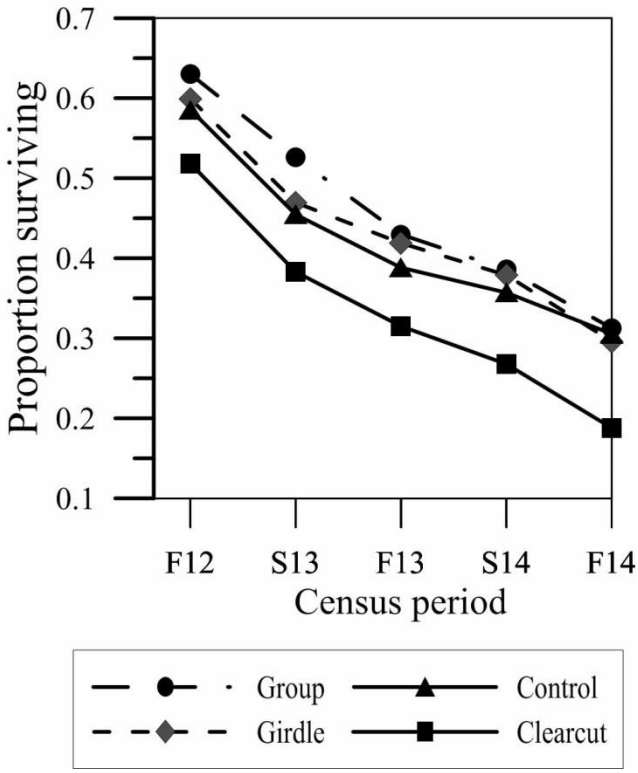

Figure 5. Plot of life table estimates showing proportion of overall seedlings planted surviving under clearcut, control, girdle and group selection treatments (mean $\pm$ 95% C.I.), with survival assessed in spring and fall, beginning fall 2012. Median life expectancy = the point at which survival falls below 0.5.

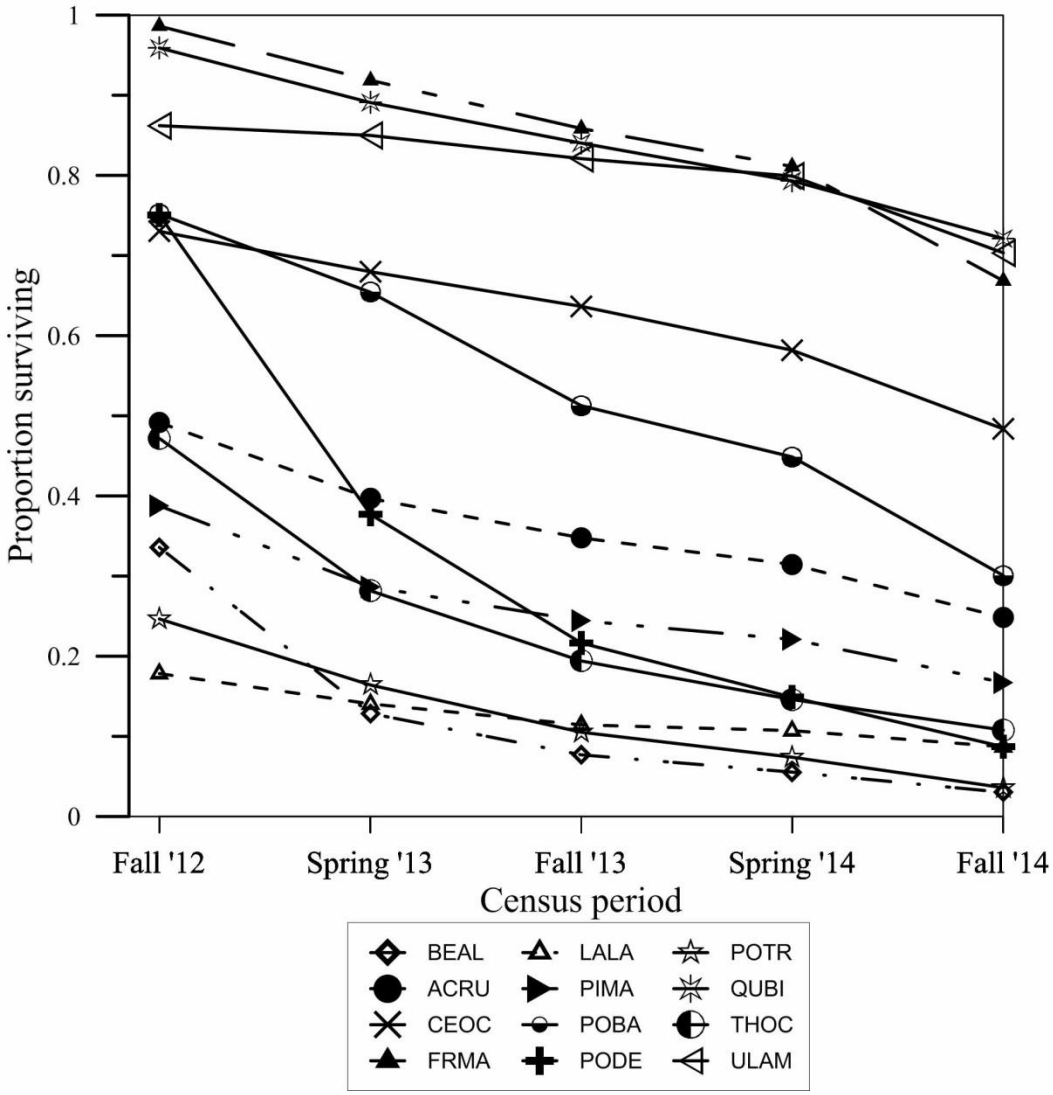

Figure 6. Plot of life table estimates of survival (mean ± 95% C.I.) for seedlings of 12 tree species, with survival assessed in spring and fall, beginning fall 2012. Median life expectancy = the point at which survival falls below 0.5. Six species entered the study with survival rates below this level, suggesting a median life expectancy of less than 1 growing season. See Table 2 for species abbreviations.

Chapter 4

Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by emerald ash borer in Minnesota, USA

Christopher E. Looney[a], Anthony W. D'Amato[b], Brian J. Palik[c], Robert A. Slesak[d]

[a] University of Minnesota, Department of Forest Resources, St. Paul, MN 55108, USA

[b] University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05095, USA

[c] USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA

[d] Minnesota Forest Resources Council, St. Paul, MN 55108, USA

Reprinted from Canadian Journal of Forest Research, Vol. 47, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer-threatened *Fraxinus nigra* forests in Minnesota, USA, pp. 183-192, © 2016 Christopher E. Looney, Anthony W. D'Amato, Brian J. Palik, Robert A. Slesak, with permission from Canadian Science Publishing. http://dx.doi.org/10.1139/cjfr-2016-0369.

1 Introduction

Fraxinus nigra Marsh. (black ash), a dominant tree species of the North American wetland forests that range from southeastern Canada (Scott 1995) to the western Great Lakes region of the U.S. and occur extensively in northern Minnesota (Erdmann et al. 1987), is imperiled by the invasive insect, emerald ash borer (*Agrilus planipennis* Fairmaire, 1888; EAB). EAB causes lethal girdling damage in all North American *Fraxinus* species (Herms and McCullough 2014). Over 99% of *Fraxinus* trees with a diameter ≥ 2.5 cm died within a decade in EAB-affected southern Michigan mixed hardwood forests (Herms and McCullough 2014), with few or no newly germinated *Fraxinus* seedlings observed on heavily infested sites (Klooster et al. 2014). While cold winter temperatures appear to slow the intensity of invasion (DeSantis et al. 2013), the regional climate is rapidly warming (Pryor et al. 2014). Thus, in a worst-case scenario, the continued spread of EAB could result in the functional loss of *F. nigra* from the wetland forests that it presently dominates (Pugh et al. 2011).

Tolerant of prolonged seasonal ponding (Erdmann et al. 1987), *F. nigra* helps to regulate ecosystem processes by lowering summer water tables through evapotranspiration, thus reducing competition from the herbaceous layer and aiding survival of associated tree species (Slesak et al. 2014). Tree species such as *Acer rubrum* L. (red maple), *Betula alleghaniensis* Britton (yellow birch), *Thuja occidentalis* L. (northern white cedar), and *Ulmus americana* L. (American elm) are often minor components of *F. nigra* forests, although advance regeneration of these species is

generally low (Palik et al. 2011). Consequently, if *F. nigra* is lost to EAB invasion, few naturally occurring species are poised to replace it (Looney et al. 2015).

Silvicultural treatments such as harvesting and seedling plantings may be critical to maintaining tree cover and ecosystem function following EAB invasion of *F. nigra* wetlands (Iverson et al. 2016). While harvest treatments can promote seedling growth by removing overstory leaf cover that blocks available light from reaching the forest floor (Smith et al. 1996), research suggests that the complete loss of the *F. nigra* overstory to preemptive salvage logging or EAB could raise the water table, invigorate the herbaceous layer, and potentially limit tree seedling establishment (Slesak et al. 2014). The creation of small gaps in the forest canopy via group selection could minimize changes in site hydrology (Slesak et al. 2014), while potentially enhancing light availability to boost seedling growth (Smith et al. 1996). However, a 2-year study in a southeastern Michigan mixed *Fraxinus* spp. forest found no increase over time in understory light availability (measured as gap fraction) in small, hydric plots following loss of the *Fraxinus* overstory (Klooster 2012). It is unclear to what degree partial harvesting or EAB-induced mortality would affect canopy openness over time in northern Minnesota's more expansive *F. nigra* wetland stands.

Beyond the threat of EAB, climate change is predicted to impact upper Great Lakes forests, potentially increasing the frequency and intensity of floods, droughts, and outbreaks of forests pests (Iverson et al. 2016). One projected effect is a reduction in growing season, wetland water budgets due to increased evapotranspiration from warming temperatures (Galatowitsch et al. 2009). Such a reduction could potentially

benefit associated tree species less tolerant of the hydric soil conditions in *F. nigra* wetlands (Iverson et al. 2016). At the same time, suitable climate locales for many tree species are predicted to shift northeastward (Iverson et al. 2008), further threatening the potential for co-occurring tree species to replace *F. nigra*. This scenario suggests that forestry-related assisted range expansion of potential *F. nigra* replacement species should be explored (Looney et al. 2015). Forestry-related assisted range expansion, which proposes northeasterly relocation of tree species within a few hundred kilometers of their current range limits (Pedlar et al. 2012), could promote species capable of maintaining both tree cover and ecosystem function while reducing future risk from climate change (Iverson et al. 2016).

While no research to date has examined the growth response of planted seedlings of non-EAB-host species in *F. nigra* forests, in a related study, we previously investigated overstory treatment effects on seedling survival (Looney et al. 2015). We found that seedling survival was lowest in clearcuts but roughly equivalent for all species except shade-intolerant *Populus balsamifera* L. (balsam poplar) in unharvested controls, group selections, and girdling treatments, the latter of which were used to emulate multiyear EAB mortality (Looney et al. 2015). Conifer species had low overall rates of survival, while a species whose native range does not presently overlap with northern *F. nigra* forests had a high rate of survival (Looney et al. 2015). However, initial seedling survival does not necessarily translate into an advantage in growth and longer-term recruitment to the sapling phase (Shipley et al. 1989).

Therefore, in the current study, we investigated the relative growth response of 10 potential *F. nigra* replacement tree species, several of which are projected to be well adapted to future climate in northern Minnesota, including two species from the next southern climate zone (Iverson et al. 2016). Seedlings were planted in *F. nigra* wetlands in four canopy treatments: control (unharvested forest), clearcut (preemptive removal of all trees), girdling of *F. nigra* (to emulate EAB mortality), and group selection (partial canopy removal to facilitate transition to replacement species). Our objectives were to determine: (1) the effects of simulated EAB-mortality and harvesting on canopy openness, as indicated by the leaf area index; (2) the influence of overstory changes from EAB and harvesting on the height and diameter relative growth rate (RGR) of planted seedlings of *F. nigra* replacement species; and (3) the most promising combination of species and treatment for management strategies to mitigate the effects of EAB under a warming future climate. We predicted that: (1) treatment intentions would be confirmed by finding canopy openness lowest in the control, low to intermediate in the group selection, high to intermediate in the girdling, and highest in the clearcut treatment, once girdling-induced *Fraxinus* mortality was complete; (2) RGR would increase with canopy openness for shade-intolerant species such as *P. balsamifera*, while shade-tolerant species such as *A. rubrum* (Niinemets and Valladares 2006) would have relatively higher RGR only in the controls; and (3) group selection and possibly girdling treatments, assuming a shelterwood effect, would support relatively high RGR for a mix of species by providing increased light while limiting the water table rise.

2 Materials and Methods

2.1 Study sites and overstory treatments

Study sites were located in *F. nigra* wetlands on the Chippewa National Forest in northern Minnesota, USA (Looney et al. 2015). Climate is continental, with most rainfall occurring during the May-September growing season (PRISM Climate Group 2015). For the 1981-2010 period, mean temperature averaged -13.7 and 16.5°C in January and July, respectively, while mean precipitation averaged 742 mm yr^{-1} (PRISM Climate Group 2015). The study sites are classified as northern wet *Fraxinus* swamp (WFn55) and northern very wet *Fraxinus* swamp (WFn64) according to native plant community classification for the state of Minnesota (MNDNR 2003). Soils within the study area are classified as Morph Series: Fine-loamy, mixed, superactive, frigid Typic Glossaqualfs and Wildwood Series: Very-fine, smectitic, nonacid, frigid Histic Humaquepts (Soil Survey Staff, Natural Resources Conservation Service, 2016). A confining clay layer and flat topography result in poor drainage and spring ponding, with water tables usually falling below the surface by mid-July (Slesak et al. 2014).

Within the study area, we identified eight experimental blocks for treatment installation. Dominant canopy tree age ranged from 150 to 274 years. Pretreatment basal area for trees >10.0 cm diameter at breast height (DBH) averaged 20.7 ± 2.2 m^2 ha^{-1}, with mean tree density of 477 ± 50.6 trees ha^{-1} (Looney et al. 2015). As the dominant overstory species, *F. nigra* comprised 91% of basal area, with minor components of *Abies balsamea* L. (balsam fir), *Populus tremuloides* Michx. (quaking aspen), *Quercus macrocarpa* Michx. (bur oak), *Tilia americana* L. (American basswood), and *U.*

americana, (Looney et al. 2015). Midstory shrub species included *Alnus incana* (L.) Moench ssp. rugosa (Du Roi) Clausen (speckled alder), *Corylus cornuta* Marshall (beaked hazel), and *Acer spicatum* Lam. (mountain maple, Looney et al. 2015).

In each block, four 1.62 ha (71.8m-radius) circular plots were established. We randomly assigned each plot to one of four treatments: control, clearcut, girdling, and group selection. The control plot was left as unharvested forest. The clearcut treatment was used to evaluate the effects of preemptive removal of all *F. nigra* prior to EAB invasion. The girdling treatment was applied to all *F. nigra* ≥ 6 cm DBH over a 2-year period to emulate multiyear EAB-induced mortality. The group selection treatment, which consisted of eight 0.04 ha ($400m^2$) circular gaps totaling approximately 20% of plot area, was used to test the efficacy of partial overstory removal to promote seedling growth while limiting the water table rise associated with clearcutting (Erdmann et al. 1987). All treatments were installed in late winter 2012 under frozen ground conditions (Looney et al. 2015).

2.2 Species selection and planting

We planted seedlings of 10 species, seven of which were native to northern Minnesota *F. nigra* forests: *Acer rubrum*, *Larix laricina* (Du Roi) K. Koch (tamarack), *Picea mariana* (Mill.) B.S.P. (black spruce), *Populus balsamifera*, *Populus deltoides* W. Bartram x Marshall (eastern cottonwood), *T. occidentalis,* and *U. americana*. We also planted two species from the next southern climate zone that are projected to have increased suitability to northern Minnesota under a warming future climate (Iverson et al.

2008): *Celtis occidentalis* L. (hackberry), which occurs in isolated populations 80 km southwest of the study area (Prasad et al. 2007), and *Quercus bicolor* Willd. (swamp white oak), an often dominant wetland forest species with a northern range limit approximately 150 km southwest of the study sites (Prasad et al. 2007). Finally, we planted seedlings of *Fraxinus mandshurica* Rupr. (Manchurian ash), an Asian species with resistance to EAB and growth form similar to *F. nigra,* which is being tested in efforts to hybridize EAB-resistant Asian/North American *Fraxinus* cultivars (Koch et al. 2012). Shade-intolerant species included *L. laricina, P. balsamifera,* and *P. deltoides,* while shade-tolerant species included *A. rubrum, C. occidentalis, F. mandshurica, P. mariana, Q. bicolor, T. occidentalis,* and *U. americana* (Niinemets and Valladares 2006). *Betula alleghaniensis* Britton (yellow birch) and *P. tremuloides* were also planted but were excluded from the growth analysis due to insufficient survival (Looney et al. 2015). Seedlings of *A. rubrum, C. occidentalis, L. laricina, P. mariana, P. deltoides,* and *T. occidentalis* were planted both before harvesting in 2011 and after harvesting in 2012. Seedlings of *Q. bicolor, P. balsamifera, F. mandshurica,* and *U. americana* were planted only after harvesting in 2012. For the 2011 plantings, we assumed that a winter snowpack would protect the seedlings from mechanical harvesting damage (Looney et al. 2015).

Seedlings of *A. rubrum, L. laricina, P. mariana, P. balsamifera, P. deltoides, and T. occidentalis* were from locally adapted seed sources, while *C. occidentalis* and *Q. bicolor* were from seed sources from adjacent climate zones. *Ulmus americana* stock was bred for tolerance to Dutch elm disease (*Ophiostoma novo-ulmi* Brasier) by USDA Forest Service researchers through controlled pollination between surviving trees on the

Chippewa National Forest and the Dutch elm disease tolerant "Valley Forge" cultivar of *U. americana* (Slavicek and Knight 2012). Chinese seed stock was used for *F. mandshurica.* All seedling stock was obtained from local commercial nurseries, with the exception of *U. americana,* which was obtained from the USFS Toumey Nursery in Watersmeet, Michigan, and *F. mandshurica,* which was obtained from a commercial nursery in Plains, Montana. Planting stock type differed among species (Table 1). Containerized seedlings were used for *C. occidentalis*, *L. laricina, P. mariana, P. balsamifera, T. occidentalis, U. americana,* and the 2011-planted *A. rubrum* (Looney et al. 2015). Bareroot seedlings were used for *F. mandshurica*, *P. deltoides Q. bicolor,* and the 2012-planted *A rubrum* (Looney et al. 2015). Stock size also differed among species (Table 1), with containerized seedlings of *P. balsamifera, C. occidentalis,* and, in particular, *U. americana* larger than seedlings of other species (Looney et al. 2015).

Six 0.04 ha (400m^2) subplots were established to serve as planting areas within each of the 1.62 ha treatment plots. We randomly distributed subplots in the control, girdling, and clearcut treatments, while in the group selection treatment, four subplots were centered in canopy gaps and two were located in the unharvested matrix. A planting bar was used to plant eight rows of seedlings on the western half of each 0.04 ha subplot. Seedlings were spaced 1.25m apart within rows, with 2.5 m between rows. Species were randomly allocated to locations within rows in each planting frame and planted on the closest favorable microsite, avoiding wet hollows as allowed by site topography. Due to delayed availability, *U. americana* and *F. mandshurica* were always located at the ends of planting rows. For all species but *U. americana,* 1,536 seedlings were planted,

distributed as 48 seedlings per species per treatment plot and 8 seedlings per species per planting subplot. For *U. americana*, 768 seedlings were planted, distributed as 24 seedlings per species per plot and 4 seedlings per subplot (Looney et al. 2015).

2.3 Data collection

2.3.1 Leaf area index

We used hemispherical photography within each treatment replicate in July 2013 and July 2015 to assess leaf area index (LAI), which was used as an indicator of overstory cover (Jonckheere et al. 2004). We used a Canon EOS 5D mark II set on aperture priority mode with a Belomo 8 mm fisheye lens, at a tripod height of 1.37 m, which yielded a field of view of 180° and circular image on the 35mm sensor format. We took photographs from 30 minutes before sunset to dusk on days with direct sun conditions. We also photographed throughout the day in overcast, diffuse sun conditions. We used a systematic sampling of 12 photo points evenly spaced within each treatment replicate and buffered 10m from treatment edge. The photo point sampling protocol was applied without variation to all treatments, including the group selection, in order to accurately assess LAI across the entire area of the treatment replicates. We used Gap Light Analyzer software (Frazer et al. 1999) to estimate LAI and processed images based on a 75° zenith angle to account for midstory foliage. Blue channel images were used to improve distinction between sunlit foliage and sky.

2.3.2 Seedling measurement

We assessed seedling root collar diameter and height in fall (September-November) 2013, one year after the final plantings, and again in 2015. We used digital calipers to obtain two opposing diameter measurements per stem, which we later averaged. For seedlings with multiple stems at soil level, we recorded the height of each stem while calculating an equivalent root collar diameter based on total stem basal area (Chojnacky and Rogers 1999). We recorded heights of each individual stem originating at or below ground level, but used the height of the tallest living stem for analytical purposes. Seedlings were assessed for the presence or absence of deer browse damage in spring 2013, 2014, and 2015.

2.4 Analytical methods

To quantify treatment effects on the overstory, we examined LAI for 2013 and 2015. The analysis of LAI included year, treatment, and year x treatment effects as potential factors in candidate models. We examined 2-year height and diameter for 2013 to 2015. We used RGR based on the differences of natural logarithms of seedling sizes in 2013 and 2015, as the response metric to help control for between-species variation in seedling size (Hunt and Cornelissen 1997). We did not find it necessary to transform height RGR, diameter RGR, or LAI to meet model assumptions. Potential predictors of RGR included species, overstory treatment, absence, or presence of browse damage in 2013, and interactions between these factors. Preliminary analysis showed that deer browse did not have a significant influence on either height or diameter RGR; therefore, we excluded browse from the final models. For LAI, as well as for seedling height and

diameter RGR, we used multilevel mixed-effects regression to analyze the blocked, repeated measures, split plot design, in which species were nested within overstory treatments. We treated individual treatment replicates as LAI sample units, with repeated LAI measurements (2013 and 2015) nested within each unit. We further analyzed the group selection treatment individually in a separate series of models to examine the effects of planting position (matrix vs. group) on seedling growth by species.

We performed mixed-effects modeling using the nlme package (Pinheiro et al. 2016) for R. For the analysis of seedling growth, random effects included the block effect, as well as seedling plots nested within blocks. For the analysis of LAI, block was the only random effect. We examined plots of model residuals vs. fitted values to evaluate model fit.

We used the Akaike information criteria (AIC) and the information-theoretic approach to evaluate model parsimony rather than base model selection on strict hypothesis tests (Burnham and Anderson 2003). We constructed multiple competing models of LAI, study-wide seedling height and diameter RGR, and seedling RGR within group selections. For each response variable, we compared models with a null, intercept-only model. For model terms with substantial AIC support, we used Tukey's HSD to make post-hoc comparisons of individual factor levels. We also report F-test results for models with high AIC support based on marginal sums of squares.

3 Results

3.1 Leaf area index by treatment

The best-supported LAI model included overstory treatment as the sole predictor but was nearly equivalent to a model that included a year term (ΔAIC = 0.22; Table 2). A model including both year and a year x treatment effect did not have substantial AIC support, defined as $\Delta AIC \leq 8$. (Burnham and Anderson 2003). In the best-supported LAI model, treatment was a significant predictor ($F=282.5$, $p<0.001$). Treatment was also a significant predictor in the second-best supported LAI model ($F=288.6$, $p<0.001$), as was the year effect ($F=10.3$, $p=0.018$). LAI was lowest in the clearcut, followed by the girdling, group selection, and control treatments (Figure 1). The model including a year effect suggested study-wide LAI increased slightly from 2013 to 2015 (Figure 1), even in the girdling treatment, where *F. nigra* mortality was not complete until 2014 and *F. nigra* sprouts were removed annually. LAI in the clearcut, girdling, and group selection treatments measured 11%, 69%, and 82% respectively of LAI in the controls (data not shown).

3.2 Overall relative growth rates by treatment

The most parsimonious models of both mean seedling height and diameter RGR for all species combined included species, treatment, and species x treatment. No other competing models for either mean overall height or diameter RGR had substantial AIC support (Δ AIC >8; Burnham and Anderson 2003). In the best-supported height RGR model, tests of species ($F= 45.1$, $p<0.001$), treatment ($F= 13.4$, $p<0.001$), and species x treatment ($F=11.1$, $p< 0.001$) were significant. The best-supported diameter RGR model also had significant tests for species ($F= 126.3$, $p<0.001$), treatment ($F= 7.4$, $p<0.001$),

and species x treatment ($F=11.0$, $p<0.001$). Within group selections, the best-supported models of both mean overall height and diameter RGR included species and planting position (gap vs. untreated matrix). No other models of mean overall height or diameter RGR within the group selections had substantial AIC support. Species was a significant predictor in both the best-supported group selection models of height RGR ($F=93.3$, $p<0.01$) and diameter RGR ($F=86.9$, $p<0.001$). Planting position was also a significant predictor in the best-supported height RGR ($F=12.4$, $p<0.001$) and diameter RGR ($F=46.7$, $p<0.001$) models.

For all species combined, the clearcut and girdling treatments had fast and relatively comparable mean height RGR (Figure 2), although mean diameter RGR was slightly slower in the girdling treatment than in the clearcut. The group selection treatment supported moderate mean overall height and diameter RGR, while mean overall height and diameter RGR in the control treatment was slow, but significantly greater than zero. Within the group selection treatment, mean overall height RGR was faster for seedlings positioned within gaps (0.76 cm cm^{-1} yr^{-1} ± 0.01) than within the untreated matrix (0.38 cm cm^{-1} yr^{-1} ± 0.01), although we found nearly equivalent support (Δ AIC = 0.97) for a model that included species but not seedling position. Mean overall diameter RGR was approximately 50% faster for seedlings planted in gaps (0.09 mm mm^{-1} yr^{-1} ± 0.01) than for seedlings planted in the matrix (0.06 mm mm^{-1} yr^{-1} ± 0.01; data not shown*).*

3.3 Species by treatment

3.3.1 Height RGR

In the control treatment, only *L. laricina, P. balsamifera*, *Q. bicolor,* and *A. rubrum* displayed mean height RGR significantly greater than zero (Figure 3). Mean height RGR for *P. deltoides, P. mariana, T. occidentalis,* and *C. occidentalis* did not significantly differ from zero, while both *U. americana* and *F. mandshurica* showed significant height loss.

In the clearcut treatment (Figure 3), *P. balsamifera* and *L. laricina* had the fastest mean height RGR, significantly faster than the third ranking species, *P. deltoides*. *Thuja occidentalis, A. rubrum, U. americana*, and *Q. bicolor* had moderate mean height RGR, whereas mean height RGR was minimal (and sometimes negative due to tip dieback) for *F. mandshurica,* and *C. occidentalis*.

Within the girdling treatment (Figure 3), the species with the fastest mean height RGR were *P. balsamifera, P. deltoides, L. laricina,* and *A. rubrum.* Mean height RGR was slower, but still significantly greater than zero, for *Q. bicolor, F. mandshurica, P. mariana, U. americana,* and *C. occidentalis*. *Thuja occidentalis* was the only species whose mean height RGR in the girdling treatment was not significantly greater than zero.

Mean height RGR by species was generally slower in the group selection than in the clearcut or girdling treatments (Figure 3). In the group selection treatment, the fastest mean height RGR occurred in *P. balsamifera, L. laricina, P. deltoides,* and *Q. bicolor.* Mean height RGR was slow but significantly greater than zero for *A. rubrum* and *T. occidentalis,* not significantly greater than zero for *P. mariana, C. occidentalis,* and *U. americana,* and negative for *F. mandshurica*.

3.3.2 Diameter RGR

In the control treatment (Figure 4), *P. balsamifera* had the fastest mean diameter RGR, followed by *A. rubrum,* and *L. laricina.* Mean diameter RGR was slow but significantly greater than zero for *Q bicolor, T. occidentalis, U. americana,* and *C. occidentalis*. Mean diameter RGR for *P. deltoides*, *P. mariana,* and *F. mandshurica* was not significantly greater than zero.

In the clearcut treatment (Figure 4), *P. balsamifera* had the fastest mean diameter RGR, followed by *P. deltoides* and *L. laricina.* Mean diameter RGR was more moderate for *Q. bicolor, U. americana, T. occidentalis, P. mariana,* and *A. rubrum*. Diameter RGR was slower but significantly greater than zero for *F. mandshurica* and *C. occidentalis*.

In the girdling treatment, *P. balsamifera*, *P. deltoides,* and *L. laricina* had the fastest mean diameter RGR (Figure 4). Mean diameter RGR was moderate for *A. rubrum, Q. bicolor*, *U. americana,* and *T. occidentalis*. *Thuja occidentalis*, *C. occidentalis*, *P. mariana,* and *F. mandshurica* had the slowest mean diameter RGR in this treatment, although their growth rates were significantly greater than zero.

In the group selection treatment, *P. balsamifera* again had the fastest mean diameter RGR, followed by *L. laricina*, *P. deltoides*, and *Q. bicolor*. Mean diameter RGR was slower, but significantly greater than zero for *A. rubrum, P. mariana, T. occidentalis, U. americana,* and *C. occidentalis*. For *F. mandshurica,* mean diameter RGR was not significantly greater than zero.

4 Discussion

Overall, we found that seedlings planted in clearcuts had the fastest mean height and diameter RGR, with growth rates generally declining as treatment LAI increased from girdling to group selection to control treatments. Mean height and diameter RGR were strongly influenced by an interaction between species and overstory treatment. In terms of individual species, *P. balsamifera* had the fastest rates of mean height and diameter RGR in all treatments except the controls, where it ranked second for height RGR. While these results suggest great potential for this species, mean RGR must be weighed against survival and projected shifts in suitable future habitat with changing climate when determining the most favorable combination of treatment and *F. nigra* replacement species to mitigate the impacts of EAB. In the discussion that follows, we consider these factors, drawing on the results of an earlier study of seedling survival from the same experiment (Looney et al. 2015).

4.1 Leaf area index and overall relative growth rates by treatment

Untreated control plots had relatively low LAI compared with other regional forest types, with mean LAI less than 50% that of nearby *A. rubrum* forests (Fassnacht and Gower 1997). While many regional *F. nigra* stands have experienced decline and canopy dieback (Palik et al. 2011), this was not the case on our study stands, so these lower values likely reflect the more open conditions of wetland forests and low tree-level LAI associated with even healthy *F. nigra* forests. Despite relatively open canopies compared with some other forest types (Fassnacht and Gower 1997), canopy cover, as

indicated by LAI, nevertheless appeared high enough to suppress mean RGR for all species, which was lower in the control than in the clearcut, girdling, or group selection treatment. Low overall mean RGR in the control contrasted with our earlier study's finding of relatively high overall survival (32.9% ± 0.7) in this treatment (Looney et al. 2015). Intact canopies may initially benefit seedling survival by suppressing competing vegetation but will hinder growth and survival over time in the boreal forest (Lieffers et al. 1996).

Clearcuts, which involved the removal of living trees and snags as well as the incidental reduction of midstory shrubs, had the lowest LAI of any treatment. Although harvested *F. nigra* vigorously resprouted (Slesak et al. 2014), LAI in clearcuts measured just 11% of LAI in unharvested controls at the end of the study. Clearcut treatments also had the highest mean overall height and diameter RGR, largely driven by shade-intolerant species, which generally perform best in the open conditions (Youngblood and Titus 1996). In contrast, our related work found that the clearcut treatment had lowest overall seedling survival (22.1% ± 0.6 compared with 30.7% ± 0.3 for all treatments combined; Looney et al. 2015). Higher initial seedling mortality but faster mean RGR in the clearcut treatment may reflect elimination of seedlings from harsher microsites (Jones and Sharitz 1998) and/or competition from an observed increase in herbaceous vegetation (Slesak et al. 2014).

The girdling treatment used to emulate multiyear EAB-induced mortality left a substantial amount of residual cover, as indicated by LAI measurements that were only 30% lower than controls. Girdling treatment LAI increased slightly along with that of

other treatments between 2013 and 2015, despite complete mortality of the *Fraxinus* canopy by 2014 and annual removal of *F. nigra* sprouts (Slesak et al. 2014). In a 2-year study, Klooster (2012) similarly found that understory light availability did not increase over time in response to EAB-induced *Fraxinus* mortality on hydric sites in southeastern Michigan forests. Because girdling did not remove midstory shrubs, their leaf production may have been stimulated by increased light, offsetting the loss of overstory LAI. Girdling treatments supported mean overall RGR second only to the clearcuts. In our earlier study, we found that girdling treatments supported overall relatively high survival (33.3% ± 0.7) of a mix of tree species (Looney et al. 2015). While Slesak et al. (2014) observed significant water table rise and high graminoid cover in clearcut treatment one year after harvesting, they noted that water table rise did not reach similar levels in the girdling treatment until the second year. The greater residual LAI of the girdle treatment also appeared to suppress herbaceous layer height growth and graminoid cover relative to the clearcut treatment (CE Looney, *unpublished data*). Depending on the intensity of infestation (Klooster et al. 2014), multiyear EAB-induced mortality could potentially provide a shelterwood effect that permits seedlings to survive to sufficient size to withstand the slightly delayed water table rise (Slesak et al. 2014).

Group selection resulted in a more moderate reduction in overstory cover, as indicated by an 18% reduction in LAI. LAI increased between years at a rate similar to that of other treatments, suggesting that rapid gap closure from lateral canopy growth did not occur. Nonetheless, the group selection treatment had the slowest mean overall RGR of any treatment but the control. In comparison, we previously found relatively

comparable overall survival in group selection (34.5% ± 0.7), girdling (33.3% ± 0.7), and control (32.9 ± 0.7; Looney et al. 2015). Because only four of the six planting subplots in the group selection treatment were situated within gaps, mean LAI above the seedlings was lower than indicated by the systematic LAI sampling, which did not directly overlap with the randomly located seedling plots. Further analysis revealed some evidence of greater mean overall RGR in gaps, but nearly equivalent AIC support for seedling species alone as the factor responsible for RGR differences within group selections. The modest gap sizes used in this treatment, the study area's high latitude, and a surrounding matrix of mature trees likely limited seedling exposure to direct sunlight (Canham et al. 1990), and, thereby, the effectiveness of this treatment in increasing RGR.

4.2 Species by treatment

Populus balsamifera had the fastest mean height RGR in all treatments except the controls, where it ranked second, as well as the fastest mean diameter RGR in all treatments. In our companion study (Looney et al. 2015) shade intolerant *P. balsamifera* had moderate overall survival (36.0% ± 1.2). These findings support the observation that, in general, rapid growth appears to promote survival in *Populus* spp. (Kobe et al. 1995). Research into age structure and gap dynamics of *Populus* stands suggests that *P. balsamifera* may regenerate in the partial sun of gaps and form uneven-aged stands (Cumming et al. 2000). Although *P. balsamifera* is generally classified as shade-intolerant (Niinemets and Valladares 2006), comparatively low LAI in *F. nigra* stands may permit growth of this species even in controls at the cost of somewhat reduced

survival (Looney et al. 2015). In contrast to the RGR and survival results, *P. balsamifera* may not be adaptable to northern Minnesota conditions under a warming climate (Iverson et al. 2008), suggesting that it may have limited long-term viability as an *F. nigra* replacement species.

The shade intolerant species, *L. laricina* (Niinemets and Valladares 2006) had among the fastest mean height and diameter RGR in every treatment, while shade intolerant *P. deltoides* (Niinemets and Valladares 2006) had fast mean height and diameter RGR in all treatments but the controls. However, in the previous study, *L. laricina* and *P. deltoides* were among the species with the lowest survival, averaging just 9.6% ± 0.8 and 11.0% ± 0.7, respectively, across all treatments (Looney et al. 2015). The small sample sizes of low-surviving species resulted in high levels of variation in RGR, as evidenced by the error bars in Figure 3.

In contrast, shade tolerant *A. rubrum* (Niinemets and Valladares 2006) had moderate mean height RGR in all treatments and fast to moderate diameter RGR in the control, girdling, and group selection treatments. Our companion study found that *A. rubrum* had above average survival in the control (33.3% ± 2.4), girdling (29.6% ± 2.3), and group selection (33.5% ± 2.4) treatments (Looney et al. 2015). The combined results are in agreement with a general understanding of shade tolerance as a trade-off between survival in low light and potential for growth in open conditions (Kobe et al. 1995). *Acer rubrum* shows plasticity in growth allocation under different light regimes, but often grows less rapidly than shade-intolerant species (Abrams 1998). *Acer rubrum* is projected

to be adapted to the future climate of northern Minnesota (Prasad et al. 2007) and, thus, could represent a relatively viable *F. nigra* replacement species.

Shade-intermediate *U. americana* (Niinemets and Valladares 2006), a species that was widespread in *F. nigra* forests before Dutch elm disease (Iverson et al. 2016), had among the highest survival (74.8% ± 2.1) of all species in all treatments in our previous study (Looney et al. 2015). In the present study, mean height RGR was moderate in clearcut and girdling treatments, but not significantly greater than zero in the control and group selection treatments. Mean diameter RGR was slow in all treatments, although significantly greater than zero. These results support the observation of Chen (1997) that height growth appears negatively correlated with shade tolerance, but the relationship between diameter growth and shade tolerance is less clear. Based on climate parameters alone, a large increase in habitat suitability and potential abundance is projected for *U. americana* in the study region as the climate warms (Iverson et al. 2016). However, although we planted Dutch elm disease-tolerant stock, it should be noted that there is a risk that the disease could overcome tolerance (Slavicek and Knight 2012). Consequently, while *U. americana* appears to be a viable *F. nigra* replacement species, it is uncertain whether planted seedlings could survive to occupy the overstory.

In addition to species native to our study ecosystems, we investigated the replacement potential of *C. occidentalis* and *Q. bicolor*, species from the next southern climate zone that are projected to be adapted to the future climate of the northern Great Lakes region (Iverson et al. 2008). Although we previously found moderately high survival for *C. occidentalis* (52.9% ± 1.3: Looney et al. 2015), the species showed limited

mean RGR in all treatments. A dendrochronological study of *C. occidentalis* at its northern range limit in Quebec found growth declines in association with low maximum temperature and heavy precipitation (Houle and Bouchard 1990). In comparison, *Q. bicolor* had high mean survival (75.5% ± 1.1; Looney et al. 2015) with moderately rapid mean height and diameter RGR across treatments, although partial overstory removal may be necessary for longer-term seedling viability in northeastern *Quercus* species (Dey et al. 2008). Positive growth under the full sun and waterlogged conditions of the clearcuts is consistent with the results of a previous study conducted within *Q. bicolor*'s natural range (Kabrick et al. 2012). At present, the northern range limit of *Q. bicolor* may be defined by insufficient degree days for flower maturation rather than lack of cold tolerance (Morin et al. 2007). Given a projected increase in the length of northern Minnesota's growing season with warming climate (Iverson et al. 2016); *Q. bicolor* could represent a viable future *F. nigra* replacement species.

Finally, we evaluated the response of *F. mandshurica*, an Asian species that is EAB-resistant, to northern Minnesota *F. nigra* forest conditions. While we previously found high survival for *F. mandshurica* (73.3 ± 1.1; Looney et al. 2015), mean height RGR for this species was significantly above zero only in the girdling treatment. A previous study of *F. mandshurica* in its native range suggests that the species may be sensitive to herbaceous competition (Wang et al. 2013). The decreased cover and delayed mortality of the girdling treatment may produce a shelterwood effect, allowing this species to outgrow the herbaceous layer prior to the senescence of the *F. nigra* canopy

(Lieffers et al. 1996). Zero or negative growth might also be due to cold damage (Chen and Chen 1999), as we observed tip dieback (CE Looney, personal observation).

4.3 Other factors affecting seedling performance

An unusually low winter snowpack in 2011-2012 may have decreased protection of 2011-planted seedlings from harvesting machinery (Looney et al. 2015). In addition, limited snowpack increases soil freezing and frost heaving (Goulet 1995). Although frost heaving would likely have resulted in the outright mortality of most seedlings, some may have survived but suffered damage from root system loss or partial excavation (Goulet 1995).

Variations in seedling stock may also have contributed to differences in performance. Containerized seedlings may have a growth advantage over bareroot stock through reduced transplant shock (Wilson et al. 2007). Larger seedlings typically exhibit more rapid growth and are able to compete more effectively with herbaceous competition for light (Jobidon et al. 1998). Stature is likely also important in *F. nigra* wetlands as it reduces submergence of aboveground tissues during seasonal ponding (Knight et al. 2012). Additionally, we were only able to evaluate a single provenance of stock for each species. Matching stock to site requirements may improve planting success (Landis et al. 2010). It is recommended that future research evaluate the potential for assisted range migration of southern genotypes of *P. balsamifera* to northern Great Lakes *F. nigra* forests, as well as explore the potential growth benefits of herbaceous understory control to reduce competition (Wang et al. 2013).

5 Conclusions

Overstory treatment, in combination with species, influenced mean height and diameter RGR of planted seedlings in *F. nigra* wetlands in northern Minnesota, USA. Clearcutting promoted rapid mean RGR, especially of shade-intolerant species, but this treatment resulted in an immediate rise in the water table (Slesak et al. 2014), as well as low overall survival (Looney et al., 2015). Furthermore, flooded hardwood markets and or future quarantines of the movement of *F. nigra* lumber may render salvage harvesting uneconomical following EAB invasion (Herms and McCullough 2014). While our previous study found that planting in controls resulted in high survival, it appears unviable for long-term growth in the absence of some disturbance. However, results for the girdling treatment suggest that planting under undisturbed canopy once EAB invasion becomes imminent in a region may produce a shelterwood effect that delays water table rise and supports relatively high growth and survival for a variety of species. Group selection was no more effective than girdling in promoting growth but could potentially offset planting costs, assuming that timber markets are available, while encouraging better survival than the clearcut treatment. Species with a combination of moderate to rapid mean height and diameter RGR and moderate to high (≥30%) survival, based on the results of our previous study, included *P. balsamifera* (all treatments), *A. rubrum* (all but the clearcut treatment), *Q. bicolor* (all treatments), *and U. americana* (clearcut and girdling treatments). When projected shifts in suitable habitat due to warming climate were also considered, *A. rubrum, Q. bicolor*, and *U. americana* appear viable under both

present and future conditions, while *P. balsamifera* may represent only a near-term solution. It should further be noted that, even if Dutch elm disease-tolerant *U. americana* stock is used, the disease could overcome tolerance (Slavicek and Knight 2012).

References

Abrams, M.D., 1998. The red maple paradox. BioScience 48, 355–364. http://dx/doi.org/10.2307/1313374.

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., and White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631. http://dx/doi.org/10.1139/x90-084.

Chen, H., 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. 27, 1383–1393. http://dx/doi.org/10.1139/x97-099.

Chen, X. and Chen, Z., 1999. Frost injury in Manchurian ash plantations. J. Northeast For. 27, 10–14.

Chojnacky, D. and Rogers, P.C., 1999. Converting tree diameter at root collar (drc) to diameter at breast height (dbh). West. J. Appl. For. 14, 14–16.

Cumming, S.G., Schmiegelow, F.K.A., and Burton, P.J., 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think. Ecol. Appl. 10, 744–759. http://dx/doi.org/10.2307/2641042.

DeSantis, R.D., Moser, W.K., Gormanson, D.D., Bartlett, M.G., Vermunt, B., 2013. Effects of climate on emerald ash borer mortality and the potential for ash survival in North America. Agric. For. Meteorol., 178–179, 120–128. http://dx/doi.org/10.1016/j.agrformet.2013.04.015.

Dey, D.C., Jacobs, D., McNabb, K., Miller, G., Baldwin, V., Foster, G., 2008. Artificial regeneration of major oak (*Quercus*) species in the eastern United States—A review of the literature. For. Sci. 54, 77–106.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NRS-P-72.

Fassnacht, K.S., Gower, S.T., 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can. J. For. Res., 27, 1058–1067. http://dx/doi.org/ 10.1139/x97-058.

Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs. Users' manual and program documentation, version 2. Simon Fraser University, Burnaby B.C. and Institute of Ecosystem Studies, Millbrook N. Y.

Galatowitsch, S., Frelich, L., Phillips-Mao, L., 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol. Conserv. 142, 2012–2022. http://dx/doi.org/10.1016/j.biocon.2009.03.030.

Goulet, F., 1995. Frost heaving of forest tree seedlings: a review. New For. 9, 67–94. http://dx/doi.org/10.1007/BF00028927.

Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59, 13–30. doi:10.1146/annurev-ento-011613-162051. PMID:24112110.

Houle, G., Bouchard, F., 1990. Hackberry (*Celtis occidentalis*) at the northeastern limit of its distribution in North America: population structure and radial growth patterns. Can. J. Bot. 68, 2685–2692. http://dx/doi.org/10.1139/b90-339.

Hunt, R., Cornelissen, J.H.C., 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol. 135, 395–417. http://dx/doi.org/10.1046/j.1469-8137.1997.00671.x.

Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx/doi.org/10.1007/s10021-015-9929-y.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage., 254, 390–406. http://dx/doi.org/10.1016/j.foreco.2007.07.023.

Jobidon, R., Charette, L., Bernier, P.Y., 1998. Initial size and competing vegetation effects on water stress and growth of Picea mariana (Mill.) BSP seedlings planted in three different environments. For. Ecol. Manag. 103, 293–305. http://dx/doi.org/10.1016/S0378-1127(97)00228-4.

Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004. Review of methods for in situ leaf area index determination: Part I. Theories, sensors and hemispherical photography. Agric. For. Meteorol. 121, 19–35. http://dx/doi.org/10.1016/j.agrformet.2003.08.027.

Jones, R.H., Sharitz, R.R., 1998. Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. J. Ecol. 86, 574–587. http://dx/doi.org/10.1046/j.1365-2745.1998.00287.x.

Kabrick, J.M., Dey, D.C., Van Sambeek, J.W., Coggeshall, M.V., Jacobs, D.F., 2012. Quantifying flooding effects on hardwood seedling survival and growth for bottomland restoration. New For. 43, 695–710. doi:10.1007/s11056-012-9331-y

Klooster, W.S., 2012. Forest responses to emerald ash borer-induced ash mortality. Ph.D. dissertation. Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH.

Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 16, 859–873. http://dx/doi.org/10.1007/s10530-013-0543-7.

Knight, K.S., Slavicek, J.M., Kappler, R., Pisarczyk, E., Wiggin, B., Menard, K., 2012. Using Dutch elm disease-tolerant elm to restore floodplains impacted by emerald ash borer, in: Proceedings of the 4th International Workshop on Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. USDA Forest

Service, Pacific Southwest Research Station, Albany, CA, Gen. Tech. Rep. PSW-GTR-240, pp. 317–323.
Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532. http://dx/doi.org/10.2307/1942040.
Koch, J.L., Carey, D.W., Knight, K.S., Poland, T.M., Herms, D.A., Mason, M.E., 2012. Breeding strategies for the development of emerald ash borer-resistant North American ash, in: Proceedings of the 4th International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. USDA Forest Service, Pacific Southwest Research Station, Albany, California, Gen. Tech. Rep. PSW-GTR-240, pp. 235–239.
Landis, T.D., Dumroese, R.K., Haase, D.L., 2010. The container nursery manual: seedling processing, storage and outplanting. Vol. 7. USDA Forest Service, Washington D.C., Agricultural Handbook 674.
Landscape Change Research Group, 2014. Landscape Change Research Group. 2014. Climate Change Atlas. Northern Research Station, U.S. Forest Service, Delaware, OH. http://www.nrs.fs.fed.us/atlas (accessed 3.3.2016).
Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., Branter, K., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286–292. http://dx/doi.org/10.5558/tfc72286-3.
Looney, C.E., D'Amato, A.W., Palik, B.J., Slesak, R.A., 2015. Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Can. J. For. Res. 45, 1728–1738. http://dx/doi.org/10.1139/cjfr-2015-0129.
MNDNR, 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, MN.
Morin, X., Augspurger, C., Chuine, I., 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology 88, 2280–2291. http://dx/doi.org/10.1890/06-1591.1.PMID:17918406.
Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. http://dx/doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2011. *Fraxinus nigra* (black ash) dieback in Minnesota: Regional variation and potential contributing factors. For. Ecol. Manag. 261, 128–135. http://dx/doi.org/10.1016/j.foreco. 2010.09.041.
Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. BioScience 62, 835–842. http://dx/doi.org/10.1525/bio.2012.62.9.10.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2016. nlme: Linear and nonlinear mixed effects models. Version 3-1. Foundation for Statistical Computing, Vienna, Austria. http://CRAN R-Proj. Orgpackage Nlme R Package Version 3–1 (accessed 3.5.2016).

PRISM Climate Group, 2015. PRISM climate data: Recent years (Jan 1981-June 2014). http://www.prism.oregonstate.edu/recent/ (accessed 1.1.2015).
Pryor, S.C., Scavia, D., Downer, C., Gaden, M., Iverson, L.R., Nordstrom, R., Patz, J., Robertson, G.P., 2014. Midwest, in: Melillo, J.., Richmond, T.C., Yohe, G.W. (Eds.), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, Washington, D.C., pp. 418–440.
Pugh, S.A., Liebhold, A.M., Morin, R.S., 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can. J. For. Res. 41, 2165–2175. http://dx/doi.org/10.1139/x11-138.
Scott, G.A.J., 1995. Canada's Vegetation: A World Perspective. McGill-Queen's Press, Montreal, Quebec.
Shipley, B., Keddy, P.A., Moore, D.R.J., Lemky, K., 1989. Regeneration and establishment strategies of emergent macrophytes. J. Ecol. 77, 1093–1110. http://dx/doi.org/10.2307/2260825.
Slavicek, J.M., Knight, K.S., 2012. Generation of American elm trees with tolerance to Dutch elm disease through controlled crosses and selection. Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel, S.J. (Eds.), Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, Gen. Tech. Rep. PSW-GTR-240, pp. 342–346.
Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx/doi.org/10.1139/cjfr-2014-0111.
Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1996. The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley and Sons, New York, NY.
Soil Survey Staff, 2016. Official soil series descriptions. USDA Nat. Resour. Conserv. Serv. http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/soils/home/?cid=nrcs142p2_053587 (accessed 12.30.2016).
Wang, J., Wu, L., Zhao, X., Fan, J., Zhang, C., Von Gadow, K., 2013. Influence of ground flora on *Fraxinus mandshurica* seedling growth on abandoned land and beneath forest canopy. Eur. J. For. Res. 132, 313–324. http://dx/doi.org/10.1007/s10342-012-0676-8.
Wilson, E.R., Vitols, K.C., Park, A., 2007. Root characteristics and growth potential of container and bare-root seedlings of red oak (Quercus rubra) in Ontario, Canada. New For. 34, 163–176. http://dx/doi.org/10.1007/s11056-007-9046-7.
Youngblood, A., Titus, B., 1996. Clearcutting — a regeneration method in the boreal forest. For. Chron. 72, 31–36. http://dx/doi.org/10.5558/tfc72031-1.

Table 1. Scientific name, tree species code, stock type, plus average mean height (± standard error (S.E.)) and average basal diameter (±S.E.) for seedlings of 10 potential *F. nigra* replacement species.

Species	Code	Stock type	Mean height (cm)	Mean basal diameter (mm)
Acer rubrum (planted 2011)	ACRU	Container (90 cm^3)	17.4 ± 4.2	3.7 ± 0.2
Acer rubrum (planted 2012)	ACRU	Bareroot (1+0)	27.5 ± 10.1	4.6 ± 0.3
Celtis occidentalis	CEOC	Container (336 cm^3)	37.4 ± 2.1	4.6 ± 0.2
Fraxinus mandshurica	FRMA	Bareroot (3+0)	68.3 ± 2.5	9.8 ± 0.3
Larix laricina	LALA	Container (60 cm^3)	44.9 ± 2.0	4.7 ± 0.2
Picea mariana	PIMA	Container (90 cm^3)	45.3 ± 1.7	4.4 ± 0.1
Populus balsamifera	POBA	Container (164 cm^3)	50.8 ± 2.8	5.0 ± 0.3
Populus deltoides	PODE	Bareroot (1+0)	60.7 ± 3.3	5.7 ± 0.3
Quercus bicolor	QUBI	Bareroot (1+0)	33.5 ± 1.5	5.3 ± 0.2
Thuja occidentalis	THOC	Container (60 cm^3)	24.2 ± 1.9	3.3 ± 0.2
Ulmus americana	ULAM	Container (1890 cm^3)	103.0 ± 3.3	11.2 ± 0.3

Note: Code=USDA Forest Service FIA tree species code. Under "stock type" values in parentheses correspond to container volume for containerized seedlings and number of years spent in nursery and transplant beds for bareroot stock. Mean height and diameter measurements were taken at the start of the growth study period in fall 2013.

Table 2. Summary of confidence set model for height and diameter RGR, based on the deviance information criteria ($\Delta AIC \leq 8$).

Response	Factors	AIC	ΔAIC	Relative likelihood	Weights	Evidence ratio
LAI	Treatment	-2.18	0.00	1.00	0.53	1.00
LAI	Treatment, year	-1.96	0.22	0.90	0.47	1.12
LAI	Null	125.75	127.93	0.00	0.00	>1000
Height RGR	Treatment, species, treatment x species	-2317.96	0.00	1.00	1.00	1.00
Height RGR	Null	-877.42	1440.54	0.00	0.00	>1000
Diameter RGR	Treatment, species, treatment x species	-9554.97	0.00	1.00	1.00	1.00
Diameter RGR	Null	-7407.23	2147.74	0.00	0.00	>1000
Diameter RGR: group selections	Species, position	-3000.1	0.00	1.00	1.00	1.00
Diameter RGR: group selections	Null	-2410.6	589.50	0.00	0.00	>1000
Height RGR: group selections	Species, position	-609.73	0.00	1.00	1.00	1.00
Height RGR: group selections	Species	-608.76	0.97	0.62	0.38	2.62
Height RGR: group selections	Null	-120.36	489.37	0.00	0.00	>1000

Note: Model terms are provided for each model, as well as information-theoretic support compared with the most plausible model in the set.

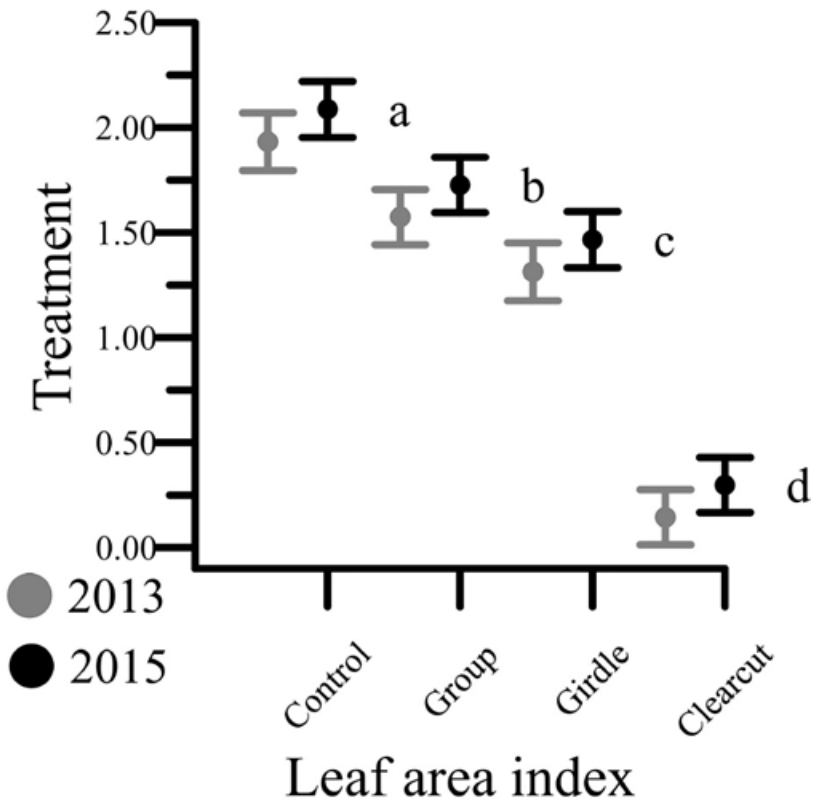

Figure 1. Mean leaf area index (LAI) for four overstory treatments (mean ± 95% confidence intervals) on *F. nigra* wetland forest study sites in northern Minnesota, USA, in the summers of 2013 and 2015. This figure illustrates the more complex, second-best supported model of LAI. The best-supported model eliminated the year effect, but treatment means over the duration of the study were intermediate between the two sets of values shown here. Letters adjacent to species summarize pairwise comparisons of treatments. Levels not connected by the same letter are significantly different ($p<0.05$).

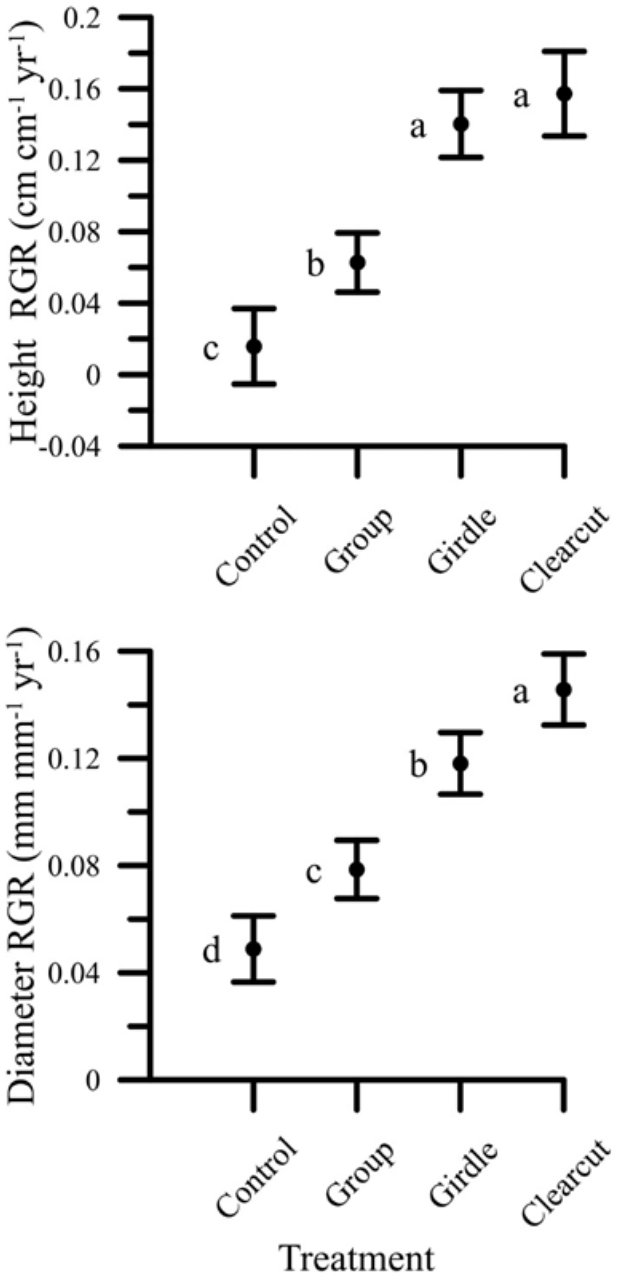

Figure 2. Mean 2-year overall relative growth rate (RGR) for height (cm cm^{-1} yr^{-1}) and diameter (mm mm^{-1} yr^{-1}) by treatment for seedlings of potential *F. nigra* replacement species planted in northern Minnesota *F. nigra* wetland forest (± 95% confidence intervals). RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of treatments. Levels not connected

by the same letter are significantly different ($p<0.05$).

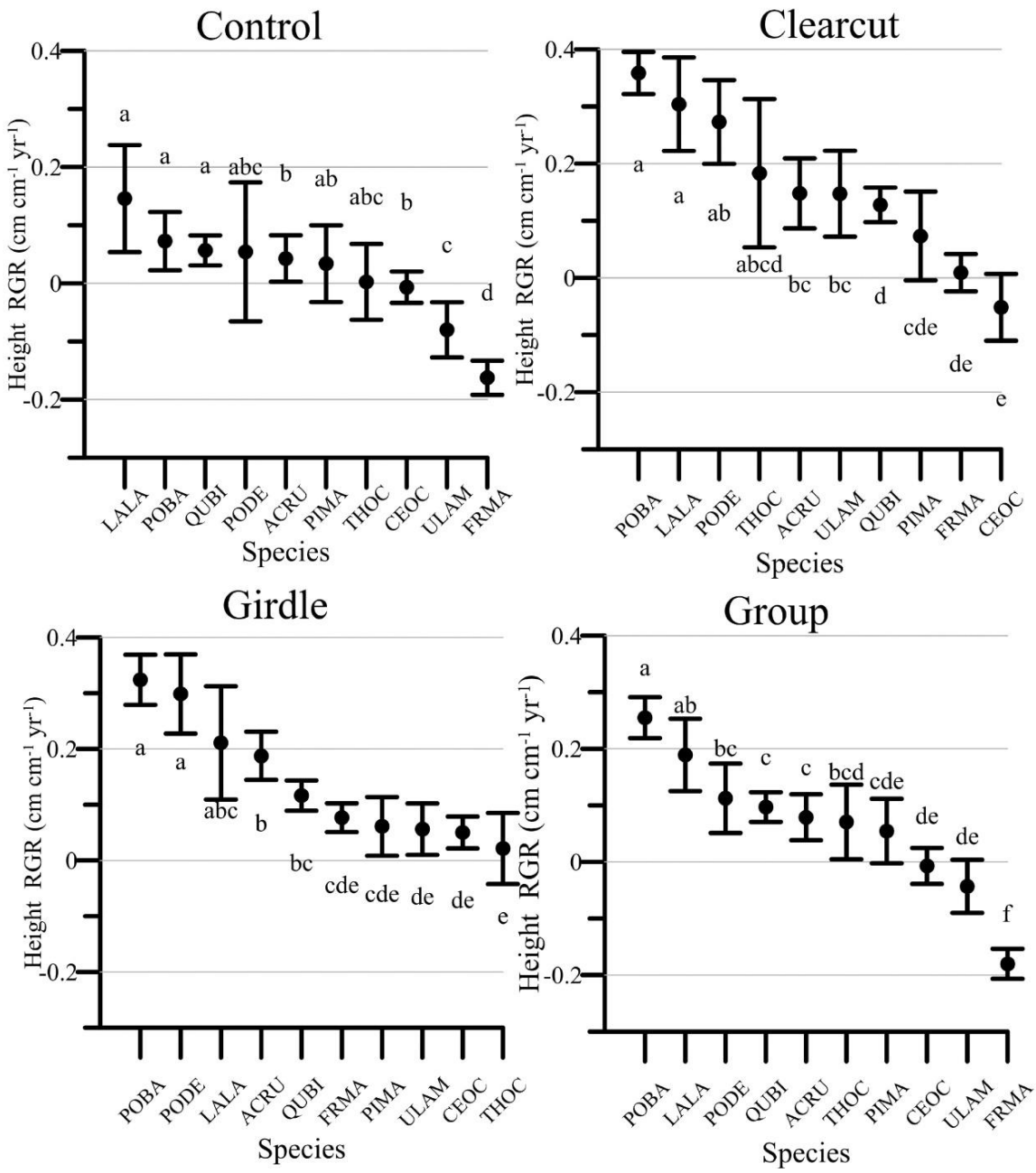

Figure 3. Interaction plot showing mean 2-year species by treatment relative growth rate (RGR) for height (cm cm^{-1} yr^{-1}; ± 95% confidence intervals) for seedlings of 10 potential *F. nigra* replacement species planted in *F. nigra* wetland forest. RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of species within treatments. Levels not connected by the same letter are significantly different ($p<0.05$). See Table 1 for species abbreviations.

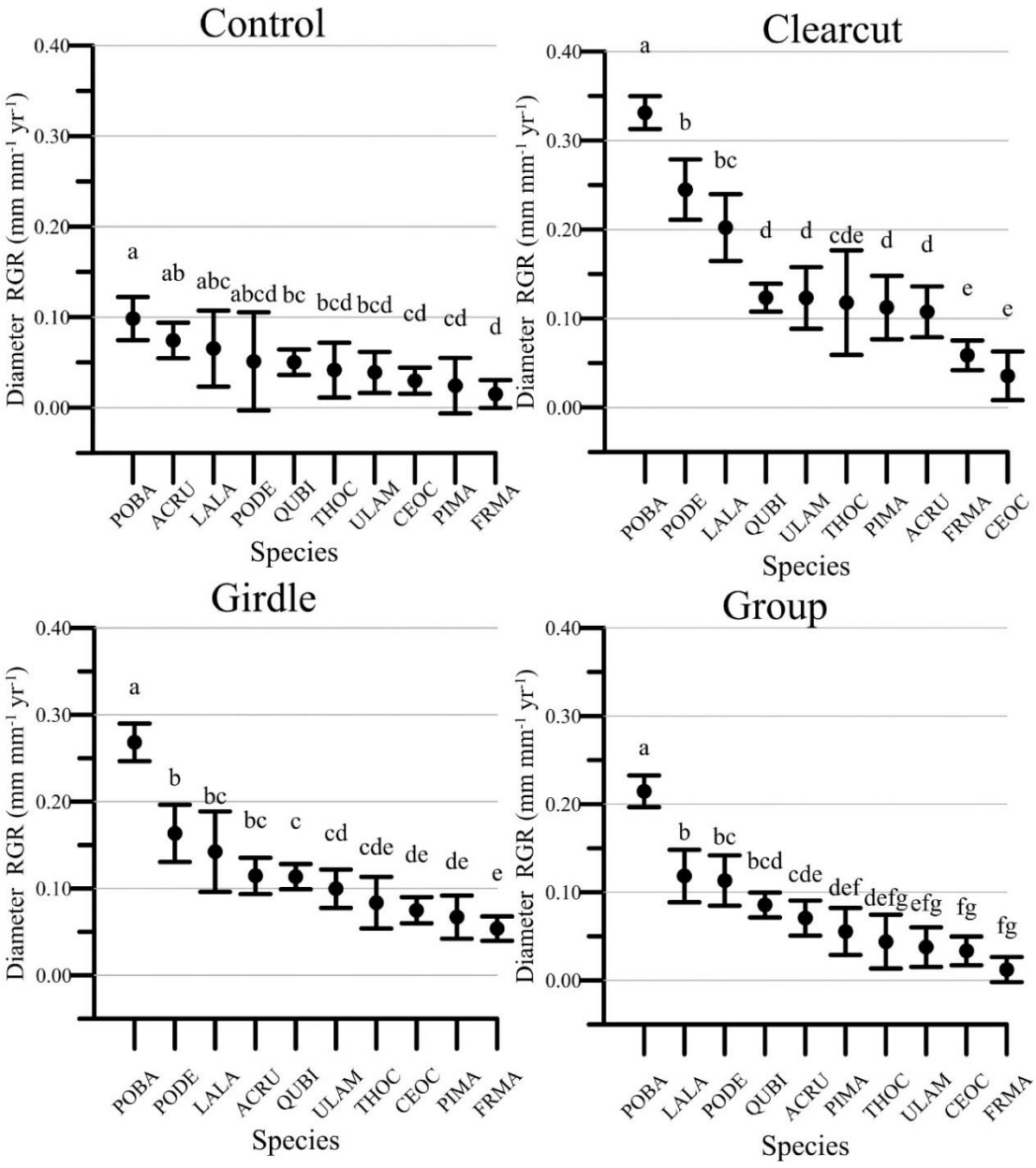

Figure 4. Interaction plot showing mean 2-year species by treatment relative growth rate (RGR) for diameter (mm mm^{-1} yr^{-1}; ± 95% confidence intervals) for seedlings of 10 potential *F. nigra* replacement species planted in *F. nigra* wetland forest. Species are displayed on the y-axis for visibility. RGR was based on fall 2015 measurements relative to fall 2013. Letters adjacent to species summarize pairwise comparisons of species within treatments. Levels not connected by the same letter are significantly different ($p<0.05$). See Table 1 for species abbreviations.

Chapter 5

The response of *Fraxinus nigra* forest ground-layer vegetation to emulated emerald ash borer mortality and management strategies in northern Minnesota, USA

Christopher E. Looney[a], Anthony W. D'Amato[b], Brian J. Palik[c], Robert A. Slesak[d], and Mitchell A. Slater[c]

[a]University of Minnesota, Department of Forest Resources, St. Paul, MN 55108, USA

[b] University of Vermont, Rubenstein School of Environment and Natural Resources, Burlington, VT 05095, USA

[c] USDA Forest Service, Northern Research Station, Grand Rapids, MN 55744, USA

[d] Minnesota Forest Resources Council, St. Paul, MN 55108, USA

Reprinted from Forest Ecology and Management, Vol. 389, Looney C.E., D'Amato A.W., Palik B.J., Slesak R.A., Slater M.A., The response of *Fraxinus nigra* forest ground-layer vegetation to emerald ash borer and management strategies in Minnesota, USA, pp. 352-363, Copyright © 2017 with permission from Elsevier. http://dx.doi.org/10.1016/j.foreco.2016.12.028.

1 Introduction

When an invasive organism targets a dominant tree species, it can trigger unprecedented shifts in forest plant communities, resulting in drastically altered ecosystem services and disturbance regimes (Orwig, 2002). In North American forests, non-native insects and diseases have functionally eliminated dominant tree species such as *Castanea dentata* (Marshall) Borkh. (American chestnut) and *Tsuga canadensis* (L.) Carrière (eastern hemlock) from all or part of their range, resulting in dramatic shifts in ecosystem composition, structure and function (Ellison et al., 2005). Due to their unique influence on resource dynamics, litter quality, and understory communities (Preisser et al., 2014), the loss of such once-dominant canopy species can result in ecosystem conditions that lack contemporary analogs, posing a challenge to long-term conservation and management (Ellison et al., 2005).

The invasive insect, emerald ash borer (EAB; *Agrilus planipennis* Fairmaire) represents a significant threat to North American *Fraxinus* (ash) species (Herms and McCullough, 2014). EAB causes lethal girdling damage as its larvae feed on the phloem and cambium of North American *Fraxinus* trees, which lack resistance to the insect (Gandhi and Herms, 2010). Less than a decade after EAB was first identified in southern Michigan, *Fraxinus* spp. trees greater than 2.5 cm in diameter experienced greater than 99% mortality (Herms and McCullough, 2014), and viable *Fraxinus* seeds were negligible to non-existent on the most heavily infested sites (Klooster et al., 2014). While the growth of associated tree species was enhanced by the loss of *Fraxinus* spp. to EAB in mixed-species upland forests (Flower et al., 2013), advance regeneration and canopy-

level individuals of associated tree species are much lower in wetland forests dominated by *Fraxinus nigra* Marsh. (black ash; Palik et al., 2012). Consequently, the continued spread of EAB could potentially result in loss of overstory cover and dramatic changes in ecosystem function in *F. nigra* forested wetlands (Iverson et al., 2016; Looney et al., 2015), which range from the western Great Lakes region (especially Minnesota) in the U.S. to southeastern Canada (Erdmann et al., 1987; Scott, 1995).

Our previous work evaluated the use of silvicultural treatments to promote artificial regeneration of non-EAB-host tree species to maintain ecosystem function following EAB invasion of *F. nigra* wetland forests (Looney et al., 2015). In many forested systems, harvest treatments can greatly enhance the potential for regeneration success (Smith et al., 1996). For example, clearcuts can aid the establishment of shade-intolerant species by opening the forest floor to sunlight (Smith et al., 1996), while group selection treatments can both improve light availability and ameliorate harsh microclimate effects (Smith et al., 1996), favoring a range of species tolerances. In *F. nigra* forests, the use of clearcutting may be problematic, as previous research suggests the loss of the *F. nigra* overstory may alter site hydrology and adversely impact the composition of both the woody and herbaceous understory plant communities (Erdmann et al., 1987; Slesak et al., 2014).

Woody plant regeneration appears to be strongly influenced by site hydrology in *F. nigra*-dominated stands, which occur on sites with heavily inundated soils and seasonal ponding (Erdmann et al., 1987; Slesak et al., 2014). In these wetland systems, *F. nigra* plays an integral role in regulating hydrology by lowering the water table through

evapotranspiration during the summer growing season, in this way aiding the survival of less moisture-tolerant plant species (Telander et al., 2015). An empirical study found loss of the *F. nigra* overstory to clearcutting and EAB (as emulated by tree girdling) resulted in a multi-year rise in the water table (Slesak et al., 2014), which observational harvesting studies suggest could favor shrubs in the absence of sufficient advance tree regeneration (Erdmann et al., 1987). In a related study that examined artificial regeneration of *F. nigra* replacement species with different canopy treatments, we found significantly lower overall seedling survival in clearcuts compared to unharvested controls, group selection, and girdling treatments (Looney et al., 2015). Survival in the girdling treatment was comparable to that in the control and group selection, despite complete senescence of the girdled trees, suggesting that slower, multi-year mortality from EAB may provide a short-term shelterwood effect (Looney et al., 2015). It is unclear whether natural tree regeneration would also benefit from this effect, as no studies to date have examined the effects of EAB- or management-induced canopy changes on natural woody plant regeneration in *F. nigra* wetlands.

Changes to the overstory can also have an impact on the composition of the herbaceous plant community (Gandhi and Herms, 2010), which may further influence tree regeneration through altered competitive dynamics and/or changing ground layer environmental conditions (Royo and Carson, 2006). For example, in North American boreal forests, clearcutting is associated with aggressive growth of the grass species, *Calamagrostis canadensis* (Michx.) P. Beauv. (bluejoint), which suppresses tree regeneration through competition and by indirectly increasing soil freezing (Lieffers et

al., 1993). Moreover, in high-latitude forests, the herbaceous layer often accounts for the majority of biodiversity (Gilliam, 2007), while contributing to aboveground net primary productivity (Nilsson and Wardle, 2005). Harvesting may threaten herbaceous layer biodiversity by both removing most of the understory and causing greater soil disturbance than natural processes (Roberts, 2004). Past experience suggests clearcutting in *F. nigra* forests could shift the composition of the herbaceous plant layer toward graminoids from its present mix of facultative and obligate wetland herbaceous species (Erdmann et al., 1987; MNDNR, 2003). Work in northwest Ohio examining mixed species forests, in which *Fraxinus pennsylvanica* Marsh. (green ash) made up 60% of the canopy trees, found both clearcutting from preemptive salvage logging and multi-year EAB-induced mortality increased the overall abundance of herbaceous plants, with clearcutting associated with more rapid environmental changes and an increase in invasive plant species (Hausman et al., 2010). In wetland forests where the *F. nigra* component often accounts for 75-90% of all tree species (MNDNR, 2003) no empirical studies have assessed the response of the herbaceous plant community to canopy changes from EAB mortality or silvicultural management.

To provide a more complete scientific basis for efforts to mitigate the effects of EAB in *F. nigra* wetland forests, we investigated the response of ground-layer vegetation to four overstory treatments: clearcut; group selection; *Fraxinus* spp. girdling; and unharvested control. Our objectives were to determine: (1) to what extent established regeneration of associated tree species can be expected to contribute to future forest cover under the various canopy treatments; (2) the impact of EAB- and management-induced

canopy changes on the overall composition of the woody vegetation community; and (3) the effect of canopy treatments on the structure and composition of the herbaceous plant layer, which in turn may feedback to influence tree regeneration.

2 Materials and Methods

2.1 Site description

Our study took place in sites established as part of a large-scale *F. nigra* wetland study on the Chippewa National Forest of northern Minnesota, USA (Looney et al., 2015). Climate is continental, with 1981-2010 mean temperatures averaging -13.7 and 16.5°C for January and July, respectively (PRISM Climate Group, 2015). Mean precipitation was 742 mm yr^{-1}, with the majority occurring during the May through September growing season (PRISM Climate Group, 2015). The sites are classified as WFn55 (northern wet *Fraxinus* swamp) grading into WFn64 (northern very wet *Fraxinus* swamp) based on the native plant community classification system developed for northern Minnesota (MNDNR, 2003). The predominant overstory species is *F. nigra,* which comprises 91% of basal area, with minor components of *Ulmus americana* L. (American elm)*, Tilia americana* L. (American basswood)*, Abies balsamea* L. (balsam fir)*, Populus tremuloides* Michx. (quaking aspen)*,* and *Quercus macrocarpa* Michx. (bur oak, Looney et al., 2015). Soils are typed as Morph Series: Fine-loamy, mixed, superactive, frigid Typic Glossaqualfs and Wildwood Series: Very-fine, smectitic, nonacid, frigid Histic Humaquepts (Soil Survey Staff, NRCS, 2016). Drainage is poor due to flat topography and a confining clay layer (Slesak et al., 2014). Ponding occurs

early in the spring-summer growing season, with water tables typically receding below the surface by mid-July (Slesak et al., 2014).

2.2 Overstory treatments

The study area was divided into 8 experimental blocks. Most stands in blocks 1-6 were predominantly even-aged, while blocks 7 and 8 had multi-aged structures (A.W. D'Amato and M.R. Reinikainen, unpublished data). Within each block, four 1.62 ha (71.8m-radius) circular stands were established, each of which received one of four treatments: (1) clearcut, involving the removal of all standing living and dead trees above 6 cm diameter at breast height (DBH); (2) group selection, consisting of eight 0.04 ha ($400m^2$) circular gaps totaling approximately 20% of the plot; (3) girdling of all *Fraxinus* spp. trees ≥6 cm DBH to emulate multi-year EAB-induced mortality; and (4) control, consisting of unharvested forest. All treatments were implemented in winter 2011-2012 under frozen ground conditions (Looney et al., 2015). Girdling was repeated during winter 2012-2013 for trees where the original treatment was ineffective to guarantee mortality.

2.3 Data collection

2.3.1 Woody vegetation

We randomly installed six 11.3m-radius ($400m^2$) plots within each treatment replicate, for a total of 48 plots per treatment. Plot centers were buffered 10m from treatment edges to avoid sampling untreated forest. Within each group selection replicate,

4 plots were located in harvested gaps and 2 in unharvested matrix. Within each plot, we established three 7 m^2 subplots for vegetation sampling 5.5m from plot center, at 0, 120, and 240 degrees. Large woody stems (≥ 0.5m height but ≤ 2.54 cm basal diameter) were tallied within each subplot. Medium-sized woody stems (height ≥ 15 cm ≤ 50 cm) and small woody stems (≤ 15 cm height) were tallied separately within a nested 1m^2 plot centered on the subplot. We distinguished between seed-origin regeneration and vegetative reproduction. Preliminary measurements found overwhelming numbers of stump-origin sprouts for species such as *F. nigra* and *Acer spicatum* Lam. (mountain maple) that made accurate tallies impractical. As a result, we recorded dense clusters of stump sprouts separately from isolated vegetative reproduction. Post-treatment woody vegetation was sampled annually in summer from 2012 to 2015.

2.3.2 Herbaceous layer vegetation

We assessed cover of herbaceous vegetation in 2013 and 2015. We sampled each treatment replicate once in each measurement year between leaf-out in late June and mid-August. We sampled herbaceous vegetation in four 0.25m^2 quadrats systematically arrayed around the woody vegetation subplots within each 400m^2 plot. As with the woody regeneration subplots, herbaceous plots were arrayed at 0°, 120°, and 240°, but were spaced 3.7 and 7.4m from plot centers to avoid measuring herbaceous vegetation that had been disturbed during woody regeneration tallies. Herbaceous cover was assessed to the species level; due to overlapping strata of foliage, cover could potentially exceed 100% within quadrats.

In September 2015, we assessed the maximum height of the herbaceous layer for the growing season to help infer to what extent the herbaceous layer may shade tree seedlings. Height was assessed at the center of each 400m^2 plot, for a total of six points per treatment replicate. We measured height with a meter stick from ground level to the top of the continuous herbaceous layer; isolated taller vegetation such as a graminoid inflorescence was ignored.

2.4 Statistical analysis

We used generalized linear mixed modeling to examine the influence of canopy treatment on tree seedling density, herbaceous height, and herbaceous cover. We created Poisson models to test for differences in counts of established (≥15cm height) regeneration among treatments for species with the potential to achieve tree stature (>10 m). Predictors included treatment, species, and their interaction, while blocks were treated as random effects. Combined counts of clustered and singly occurring vegetative as well as seed-origin sprouts within individual plots and subplots were aggregated to the level of treatment replicates, which served as sample units. Species not occurring in all blocks were eliminated from the Poisson models to achieve convergence and avoid over-dispersion. These species included *F. pennsylvanica, Acer rubrum* L. (red maple), *Picea glauca* (Moench) Voss (white spruce), and *Acer negundo* L. (box elder), which had mean regeneration densities of 101.4 (± 30.4), 44.9 (± 17.6), 7.5 (± 4.3), and 36.5 (± 4.3) stems ha^{-1}, respectively. These species were included in all other analyses. For the Poisson models, we assessed model fit using Poissonness plots and comparisons with zero-

inflated models in the case of over-dispersion. For herbaceous height and cover, we used Gaussian models to evaluate treatment effects. For both sets of models, we examined plots of residuals vs. fitted values to assess model fit. The lme4 package (Bates et al., 2015) for R (R Core Team, 2013) was used for all analyses. Post-hoc comparisons using Tukey's HSD were used to examine differences between individual treatment levels or species in the event of a significant test result in both woody and herbaceous models. In the event of significant interactions between treatment and species in the analysis of tree seedling density, we used the lsmeans package (Lenth, 2016) to compare treatments within species.

We graphically examined gradients of woody and herbaceous community composition among treatments and over time using nonmetric multidimensional scaling ordination (Kruskal, 1964). We examined woody and herbaceous community matrices separately. The community matrix for woody vegetation included data measured annually from 2012 to 2015, while the herbaceous vegetation matrix included data from both the 2013 and 2015 measurements. For woody vegetation, vegetative sprouts (including stump sprout clusters), and seed-origin stems of species were treated as separate variables, due to potential differences in regeneration niche between these classes (Tardif and Bergeron, 1999). We also treated the size classes of a single species (large $\geq$ 0.5m height and $\leq$ 2.54 cm basal diameter; medium $\geq$ 15 cm $\leq$ .5m height; small $\leq$ 15 cm height) as separate variables due to ontogenetic changes in species/habitat relationships (Shipley et al., 1989).

For both woody and herbaceous species matrices, rows consisted of treatment

replicates, which served as sample units, while columns consisted of individual species and regeneration classes. Due to sparsity of species within subplots, data were aggregated to the level of treatment replicates as per the analysis of tree seedling density. We relativized data by column totals to examine both rare and common species on a more comparable basis (McCune et al., 2002; Peck, 2010). Initial ordination runs with all species had high stress and instability. Therefore, to reduce noise, we eliminated woody species regeneration classes and herbaceous plant species that occurred in less than 5% of sample units (McCune et al., 2002). Under this criterion, 10 regeneration classes of woody species, representing a mean of 263.8 (± 53.5) stems ha^{-1} or 0.3% (±0.00) of total stem density, and 28 herbaceous species, together averaging 3.5% (± 0.03) of total cover, were eliminated prior to analysis. Matrices with these species omitted were also used for PERMANOVA and indicator species analysis. We used Bray-Curtis distances for all ordinations, with 250 iterations and a stress improvement criterion of 5 for selecting axis number in Autopilot mode in PC-ORD v. 6.0 (McCune and Medford, 2011). We used Monte Carlo tests with 250 runs to evaluate axis significance (α=0.05). After verifying stability, dimensionality, and significance, we reran ordinations using 500 runs with real data (McCune et al., 2002). Ordinations were rotated to orthogonal principle axes (Peck, 2010). We examined relationships between ordination axes, individual species, and species traits using biplot overlays with a cutoff R^2 of 0.2. (McCune et al., 2002).

To aid in interpreting ordinations, we investigated additional explanatory and descriptive variables using biplots. We calculated species richness, evenness, and diversity (Shannon's H') of both woody regeneration and the herbaceous layer.

Vegetative and seed-origin seedlings were combined for diversity calculations. In addition, we summarized species responses by categorizing individual species into non-exclusive groups based on soft traits (Lavorel and Garnier, 2002). Woody species traits included shade tolerance (0-5 scale), waterlogging tolerance (0-5 scale), drought tolerance (0-5 scale), and wetland indicator status (0-3 scale; Lichvar et al., 2016; Niinemets and Valladares, 2006). Herbaceous traits included life form (forb, graminoid, fern, horestail, or vine; "The PLANTS database," 2016), wetland indicator status (Lichvar et al., 2016), and shade tolerance ("Minnesota Wildflowers," 2016; "Native Plant Information Network," 2016; "The PLANTS database," 2016). We simplified herbaceous shade tolerance ratings to a 1-3 scale, given the lack of detailed information for many species. Species listed as growing under both sun and shade were classified as intermediate (score of 2). Average trait values were calculated based on weighted averages combining species' trait values with their relative abundance. We used overlays to plot mean treatment and block positions (±S.E.) in ordination space, in order to assess the effects of these factors. For woody species, data for 2012-2015 were pooled to calculate a single periodic mean for each treatment level or block number. We also calculated interannual treatment means in order to create successional trajectories of woody communities across time. For herbaceous data, treatments and blocks were calculated separately for the 2013 and 2015 datasets. Species richness, evenness, and diversity were calculated based on all species in the woody and herbaceous community datasets, prior to deletion of rare species. To restrict inferences based on species traits to the species used in the multivariate analyses, mean trait values were calculated after

deletion of species occurring in less than 5% of sample units.

We used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to test for treatment effects on woody and herbaceous communities in 2015. This procedure permits the use of linear modeling of community distance matrices. We performed PERMANOVA in PC-ORD version 6.0 (McCune and Medford, 2011). In the event of a significant treatment effect, we performed post-hoc pairwise comparisons with Bonferroni corrections. Distance matrices were prepared identically to those used in ordinations, although restricted to species present in 2015. Permutational significance tests were based on 4999 iterations.

As a follow-up analysis, we performed blocked indicator species analysis (ISA) of both the woody and herbaceous communities in PC-ORD version 6.0 (McCune and Medford, 2011). This analysis calculates indicator values based on proportional representation of a species within a single group, compared to a species' prevalence across all groups (McCune et al., 2002). Indicator values potentially range from 0 (no treatment association) to 100 (perfect treatment association). Observed indicator values are compared to expected values derived from random permutations (n=4999) to test significance. This analysis was performed for 2015 only, using the same species matrices as for PERMANOVA.

3 Results

3.1 Woody vegetation

3.1.1 Established tree regeneration: Treatment effect

In the analysis of 2015 established tree regeneration, there was a significant main effect for treatment ($F= 839.83$, $p<0.001$) on total seedling density. For all six species combined, mean total seedling density in the clearcut was significantly higher than in other treatments (Table 1), followed by the group selection and control treatments, which had total densities that were not significantly different from each other. The girdling treatment had the lowest overall density, which was significantly lower than the clearcut and group selection but not the control.

3.1.2 Established tree regeneration: Species effect

Density of tree seedlings ≥ 15 cm in height also varied significantly by species ($F= 924.3$, $p<0.001$). Mean density of *F. nigra* was significantly higher than any other species (Table 1), followed by *U. americana,* which was significantly more abundant than any species other than *F. nigra.* We found moderate seedling density for *Q. macrocarpa.* There was no significant difference between *Populus balsamifera* L. (balsam poplar), *T. americana,* and *P. tremuloides,* the three species with the lowest seedling density.

3.1.3 Established tree regeneration: Treatment x species effect

There was also a significant species by treatment interaction effect ($F=31.66$, $p<0.001$, Table 1). The three species with highest overall abundance, *F. nigra, U. americana,* and *Q. macrocarpa,* exhibited different patterns of abundance across treatments. *Fraxinus nigra* seedling density was highest in the clearcut treatment,

followed by the group selection, control, and girdle. All treatments had significantly different *F. nigra* densities in pairwise comparisons (Table 1). In contrast, *U. americana* densities were not significantly different across treatments. *Quercus macrocarpa* seedling density was significantly higher in the control than in the group selection and girdle treatments, which were also significantly different from each other in pairwise comparisons. *Quercus macrocarpa* had its second highest seedling density in the clearcut treatment, which was not significantly different from the control and group selection.

The less abundant species, *P. balsamifera*, *T. americana*, and *P. tremuloides*, also differed in their patterns of abundance across treatments. *Populus balsamifera* density in the control was not significantly different from the group selection but was significantly higher than in the girdling treatment. *Tilia americana* density was significantly higher in the group selection than in the clearcut, girdling, and control treatments, which were not significantly different from one another in pairwise comparisons. Finally, *P. tremuloides* seedling density was equivalent in the clearcut and girdle treatment which were, in turn, significantly higher than both the control or group selection treatment.

3.1.4 Woody vegetation community ordination

For shrub and tree communities with stems ≤ 15 cm in height included (measured annually post-treatment in 2012-2015), the NMS ordination yielded a 3-dimensional solution (final stress=19.01, 145 iterations, final instability < 0.001). *Cornus sericea* L. (redosier dogwood) and *Alnus incana* (L.) Moench subsp. *rugosa* (Du Roi) R.T. Clausen (speckled alder) were more abundant in the positive portion of the first axis (variance

represented = 31.1%), while *Q. macrocarpa*, *Prunus virginiana* L. (chokecherry), *Corylus cornuta* Marshall (beaked hazelnut), and *T. americana* were more abundant in the negative portion (Figure 1). The positive portion of axis 2 was associated with *F. nigra* stump sprouts clusters (variance represented = 18.1%), while seed-origin *T. americana* and *P. glauca* were more common in the negative portion of this axis. *Quercus macrocarpa* and *Acer spicatum* increased along the third axis (variance represented=17.8%), while woody *Ribes* spp. declined (data not shown). Because this axis represented the least variance and was less interpretable, we focus only on the results for first two axes.

Biplot overlays suggested the positive portion of the first ordination axis was associated with large stems of species tolerant of flood-induced waterlogging, while the negative portion was associated with large stems of shade-tolerant species (Figure 1). The mean position of each treatment, based on pooled 2012-2015 data, was distinct in ordination space (Figure 1). The clearcut treatment was located in the positive portion of axis 2, which was associated with greater abundance of medium-sized stems of species with higher wetland indicator status. The girdling treatment was located in the negative portion of axis 2, which was associated with large seed-origin regeneration of *P. glauca*, *T. americana*, and *U. americana*, as well as the shrub species, *Alnus incana* subsp. *rugosa* and *Acer spicatum*. The control and group selection treatments were located in the neutral portion of this axis.

The mean positions of blocks, based on pooled 2012-2015 data, were also frequently distinct in the ordination (Figure 2). Blocks 4, 5, and 6 were located in the

positive portion of axis 1, which was associated with large stems of waterlogging-tolerant species such as *A. incana* and *C. sericea.* Blocks 7 and 8 were located in the negative portion of axis 1, which was associated with large stems of shade-tolerant species such as *P. virginiana* and *C. cornuta*. Blocks 1, 2, and 3 were associated with the neutral portion of axis 1.

We also found distinct successional trajectories of treatments during the 2012-2015 post-treatment period (Figure 3). Between 2012 and 2015, the girdle, group selection, and clearcut treatment became more closely associated with the positive portion of axis 1. This shift coincided with decreasing upland species density and increasing waterlogging-tolerant species such as *Alnus incana* and *Cornus sericea*. The girdle, group selection, and clearcut treatments also shifted towards the negative end of axis 2, coinciding with greater abundance of bottomland tree species, including trees such as *P. glauca* and *T. americana,* and bottomland shrubs such as *Alnus incana* and *Acer spicatum.* The control showed minimal movement along either axis.

Based on PERMANOVA results, woody community composition differed significantly among treatments in 2015 ($F=2.55$, $p=0.001$). In Bonferroni-corrected pairwise comparisons (6 comparisons; critical p-value = 0.0083), woody community composition was significantly different only between clearcuts and girdles ($p=0.0078$).

There were several woody species treatment indicators in 2015 (Table 2). Both large *F. nigra* stump-origin sprout clusters and large singly occurring vegetative sprouts were indicators of clearcuts (IV=62.3, $p = 0.001$ and IV= 66.0, $p = 0.002$, respectively). Within the girdle treatment, large seed-origin *Acer spicatum* was a significant indicator

(IV= 49.4, p= 0.037), while large seed-origin *F. nigra* (IV=39.6, p=0.042) was an indicator of group selections.

3.2 Herbaceous layer vegetation

3.2.1 Herbaceous layer height and cover

Treatment had a significant influence on 2015 herbaceous layer height (F=82.3, p<0.001), but did not significantly impact total cover (F=2.57, p=0.08, data not shown). The height of the herbaceous layer was significantly greater in the clearcut (95.2 ± 2.5 cm) than in the girdle (76.4 cm ± 2.8) or group selection treatment (70.8 cm ± 3.1). The control (40.9 cm ± 1.5) had the lowest mean herbaceous layer height of any treatment. Cover averaged 294% ± 20 in the girdle, 235% ± 23 in the control, 227% ± 20 in the group selection, and 219% ± 22 clearcut treatment.

3.2.2 Herbaceous layer ordination

The NMS ordination of 2013 and 2015 herbaceous community measurements produced a 3-dimensional solution (Final stress = 17.43, 67 iterations, final instability <0.001). The first axis represented the most variation (41.7 %). The positive portion of axis 1 was associated with *Onoclea sensibilis* L. (sensitive fern), *Impatiens capensis* Merrb. (jewelweed), and *Carex lacustris* Willd. (hairy sedge), while species associated with the negative portion of this axis included *Equisetum pratense* Ehrh. (meadow horsetail), *Laportea canadensis* (L.) Weddell (Canadian woodnettle), *Dryopteris carthusiana* (Vill.) H.P. Fuchs (spinulose woodfern), *Mitella nuda* L. (naked miterwort),

Rubus pubescens Raf. (dwarf raspberry), *Thalictrum dioicum* L. (early meadow-rue), *Fragaria virginiana* Duchesne (Virginia strawberry), *Asarum canadense* L. (Canadian wild ginger), and *Streptopus lanceolatus* (Aiton) Reveal var. *longipes (*Fernald) Reveal (twisted stalk; Figure 4). The positive portion of axis 2 was associated with forb species, including *Solidago gigantea* Aiton (giant goldenrod), *Polygonum arifolium* L. (halberdleaf tearthumb), *Crepis tectorum* L. (narrowleaf hawksbeard), and *Athyrium filix-femina* L. Roth (common ladyfern), as well as the sedge, *Carex praegracilis* W. Boott (clustered field sedge; variance represented =17.4%; Figure 4). Only *Galium trifolium* Michx. (fragrant bedstraw) was associated with the negative portion of axis 2. The third axis represented minor variation in species composition, with *Viola* spp. (violet) associated with the positive and *Caltha palustris* L. (yellow marsh marigold) associated with the negative portion of this axis (variance represented=14.3%; data not shown).

In ordination biplot overlays, the positive portion of axis 1 was associated with greater abundance of graminoid cover, while the negative portion was associated with wetland indicator species, horsetails, and ferns (Figure 4). The group selection and clearcut treatments were associated with the positive portion of this axis in both 2013 and 2015. The control and girdle treatments were associated with the negative portion of axis 1 in 2013, becoming more neutral in 2015. Forb cover was associated with the positive portion of axis 2, while other species groups showed no consistent trends. Between 2013 and 2015, all treatments shifted from the negative to the positive portion of axis 2, indicating a general increase in species richness, species diversity, and graminoid cover,

with specific increases in *Athyrium filix-femina, Crepis tectorum,* and *Carex praegracilis.* Blocks did not show a relationship with either ordination axis.

In 2015, treatment had a significant effect on herbaceous composition in PERMANOVA ($F=2.05$, $p<0.001$). In pairwise comparisons, the clearcut was significantly different from the control ($p=0.007$) and girdle ($p=0.008$) treatments, but not significantly different from the group selection treatment. No other pairwise comparisons were significant with Bonferroni corrections (6 comparisons; critical p-value =0.0083).

In 2015, there were several significant herbaceous treatment indicator species (Table 2). The grass, *Calamagrostis canadensis* **(**IV= 50.4, $p=0.001$), was an indicator of the clearcut, while the forb, *Geum rivale* L. (purple avens; IV=35.3, $p=0.04$), was a significant indicator of control treatment. Three species were indicators of the girdle treatment: *Arisaema triphyllum* (L.) Schott (Jack in the pulpit; IV= 52.3 $p=0.01$), *Carex radiata* (Wahlenb.) Small (eastern star sedge; IV=51.5, $p=0.02$), and *Matteuccia struthiopteris* (L.) Todaro (ostrich fern; IV= 39.6, $p=0.04$). There were no significant indicators for the group selection treatment.

4 Discussion

The loss of a dominant tree species to invasive organisms may result in rapid shifts in function, structure, and biological diversity, particularly in ecosystems with low canopy tree diversity (Ellison et al., 2005). While silvicultural management can be used to guide succession and influence the direction of these shifts (Waring and O'Hara, 2005), management strategies can nonetheless have unintended and potentially adverse

consequences on other ecosystem components, including ground layer communities. Thus far, strategies to manage the effects of EAB in *F. nigra* wetland forests have focused on promoting regeneration of associated tree species to maintain tree cover (Looney et al., 2015). We discuss below the complex changes observed in *F. nigra* forest ground-layer plant communities from harvesting and simulated EAB mortality, changes which highlight the importance of taking into consideration not only the impacts of EAB, but also the ecosystem-wide effects of associated management strategies designed to address overstory impacts.

4.1 Woody vegetation

4.1.1 Established tree regeneration

Based on seedling density, established tree regeneration in the *F. nigra* wetland forests examined was confined to six major species: *F. nigra, U. americana, Q. macrocarpa, P. balsamifera, P. tremuloides,* and *T. americana.* The limited regeneration density of tree species besides *F. nigra* is consistent with previous research on regional *F. nigra* forests (Palik et al., 2012). While Erdmann et al. (1987) recommended at least 12,500 *F. nigra* seedlings ha^{-1} to guarantee restocking of harvested stands, the combined density of alternate species fell far short of this figure regardless of treatment, suggesting that these other species will not readily fill growing space vacated by *F. nigra*.

The clearcut supported significantly higher mean total regeneration densities than other treatments. While lower than the clearcut treatment, total seedling densities in the group selection were also significantly higher than in the girdle treatment, but not

significantly different from the control. Seedling densities in both the clearcut and group selection treatments were largely driven by the regeneration response of *F. nigra,* which had the highest seedling density of any species in this study. High *F. nigra* seedling density in the two harvesting treatments reflected the vigorous post-harvesting sprouting response reported in previous studies of *F. nigra* regeneration (Erdmann et al., 1987). *Fraxinus nigra* showed lower but still relatively abundant established regeneration in the undisturbed control treatment, and much lower established regeneration in the girdle treatment, despite the complete mortality of the *Fraxinus* overstory by 2014 (Slesak et al., 2014). Kashian and Witter (2011) found *Fraxinus* spp. regeneration declined across multiple sites in southern Michigan mixed species forests following EAB invasion, while Klooster et al. (2014) found newly germinated *Fraxinus* seedlings almost non-existent in heavily infested Michigan and Ohio mixed *Fraxinus* stands. Both studies attributed the decline in *Fraxinus* regeneration to depletion of the seed bank following overstory mortality (Kashian and Witter, 2011; Klooster et al., 2014).

Ulmus americana was the second most abundant species after *F. nigra* across all treatments. Formerly a common species of regional wetland hardwood forests, *U. americana* may still grow to reproductive size but typically succumbs to Dutch Elm disease (*Ophiostoma novo-ulmi* Brasier) prior to reaching the overstory (Barnes, 1976). The fact that *U. americana* seedling density did not vary significantly across treatments and nearly equaled that of *F. nigra* in the girdling treatment suggests *U. americana* could be relatively more versatile than other species in the aftermath of EAB.

Seedling density of the third most abundant species, *Q. macrocarpa*, was highest in the control and lowest in the girdling treatment, while density in the clearcut treatment overlapped statistically with both that of the slightly higher control and slightly lower group selection treatment. In the northeastern U.S., overstory cover may promote the initial survival of *Quercus* species, although subsequent removal of the overstory may be necessary for sapling recruitment (Dey et al., 2008). The variation in *Q. macrocarpa* seedling density among treatments suggests advance regeneration, which is often critical to successful regeneration of *Quercus* species (Hannah, 1987), may influence *Q. macrocarpa* persistence in *F. nigra* forests. Seedling density of *Q. macrocarpa* was significantly lower in the girdling treatment than in the control or clearcut treatment, negating the hypothesis in our previous study that girdling may produce a short-term shelterwood affect that promotes seedling survival (Looney et al., 2015). A combination of water table rise and invigorated shrub and herbaceous competition may have contributed to lower *Q. macrocarpa* density in this treatment. Regionally, shelterwood harvests may fail to stimulate tree regeneration as a result of increased shrub growth (Hannah, 1988).

Populus balsamifera, T. americana and *P. tremuloides* were statistically similar and had the lowest established seedling density. *Tilia americana* achieved high mean seedling density only in the group selection treatment, perhaps aided by a combination of shade tolerance (Niinemets and Valladares, 2006) and vigorous stump sprouting response (Tredici, 2001). The large, immobile seed of *T. americana* (Cowell et al., 2010) may have limited its dispersal into the clearcuts. Established seedling density of *P. balsamifera* was

significantly higher in the clearcut than in any other treatment, while *P. tremuloides* had the highest established seedling density in the clearcut and girdling treatments. Previous work in these systems indicated LAI values for the clearcut, girdling and group selection treatments were 11%, 69%, and 82% of controls, respectively (Looney et al., 2016). The suckering response of the two shade-intolerant *Populus* species appears to be stimulated by increased solar heating of the soil, as well as lack of hormonal suppression from adult trees (Doucet, 1989; Zasada et al., 1981). Neither *P. tremuloides* nor *P. balsamifera* showed high regeneration density in the group selection, where suckering may have been inhibited by unharvested edge trees (Doucet, 1989), given the relatively small size ($400m^2$) of the gaps. While group selection may potentially reduce growing season length through the formation of cold air sinks (McDonald and Abbott, 1994), data on 2015 minimum temperatures indicated that only the clearcuts were significantly colder than other treatments (R.A. Slesak, *unpublished data*).

4.1.2 Woody vegetation community

The main gradient of variation in the woody ground-layer community, which included all size classes (<15cm height to >0.5m but <2.5cm basal diameter) of trees and shrubs, appeared to be driven by differences between experimental blocks rather than overstory treatment. Based on plant wetland indicator status, the differences among blocks appeared to reflect variation in site hydrology and stand history. Blocks 7 and 8 were associated with species with lower tolerance to waterlogging and higher shade tolerance such as *Prunus virginiana*. These blocks were characterized by shorter duration

of seasonal ponding compared with the other study sites (R.A. Slesak, unpublished data). In contrast, we observed standing water as late as August in blocks 4, 5 and 6 (C.E. Looney, personal observation), which were associated with species with higher waterlogging tolerance, principally the shrubs, *Alnus incana* and *Cornus sericia*. This finding is in agreement with Keddy and MacLellan's (1990) centrifugal forest composition model, which suggests that increasing waterlogging stress and disturbance cause *F. nigra* community composition to shift from shade-tolerant, upland species to less productive, shrub-dominated systems. Heinselman (1963) described a similar transition in regional minerotrophic swamps, with topographic transitions from uplands to peatlands corresponding with the change of mixed forest to *Alnus incana*.

The second gradient of variation in the woody layer ground community was driven by overstory treatment, with the girdling treatment and control associated with bottomland shrubs, while the group selection and clearcut treatments were associated with high densities of resprouting *F. nigra.* Heinselman (1963) reported that harvested swamp forests in the region commonly convert to *Alnus incana* thickets, while silvicultural experience with *F. nigra* suggests increased site moisture from harvesting could lead to a compositional shift toward graminoid and shrub species (Erdmann et al., 1987). Slesak et al. (2014) found that water tables rose immediately after treatment in the clearcut, while the girdling treatment showed a similar response two years post-treatment.

Based on PERMANOVA results, the woody vegetation community in the control was not significantly different from that in the girdling treatment in 2015. EAB mortality and the girdling treatment that emulated it differ from the harvesting treatments both in

the multi-year decline of the overstory (Klooster et al., 2014) and lack of incidental damage to shrubs from harvesting. In this respect, the short-term effects of EAB-girdling may be similar to wind disturbance or native insect defoliation, which also reduces the overstory canopy while preserving much of the shrub layer (Roberts, 2004). Girdling also appears to moderate changes in microclimate by lessening temperature fluctuations (Slesak et al., 2014). The ordination showed the girdling treatment had higher densities of large stems of the midstory shrub species, *Acer spicatum* and *Alnus incana*, compared to the control. In canopy gaps created by EAB mortality in upland mixed-species forests, midstory shrubs were also found to increase, which suppressed tree regeneration (Klooster, 2012).

Both the ordination and indicator species analysis showed the clearcut treatment was characterized by *F. nigra* stump sprouts. While Heinselman (1963) reported presettlement swamp forests, including those dominated by *F. nigra*, often converted to shrublands following harvest, most of the stands examined in this study were previously harvested in the early 1900s. The single treatment replicate that showed low sprouting response to clearcutting was part of block 7, an old-growth stand. The ability of trees to produce stump sprouts commonly declines with age (Tredici, 2001), so older stands may be at greater risk of water table rise and ecosystem conversion from overstory loss. The vigorous sprouting response in the clearcut treatment in this study may have moderated water table rise (Slesak et al., 2014). While sprouting *F. nigra* will likely not survive to reproductive size prior to EAB reinfestation (Aubin et al., 2015), sprouts may nevertheless aid post-EAB succession by moderating water table rise. PERMANOVA

results for 2015 indicate the clearcut treatment did not significantly differ from the group selection treatment in terms of woody species composition. While the group selection treatment also supported *F. nigra* stump sprouts, densities were lower than in the clearcuts, perhaps reflecting that only four of the six sample plots in each treatment replicate were positioned in gaps.

Between 2012 and 2015, the clearcut and group selection treatments shifted from dominance by *F. nigra* stump sprouts to increased prevalence of seed-origin tree species such as *U. americana, P. glauca,* and *T. americana.* The first year of this study, 2012, was exceptionally dry, while subsequent years had heavier precipitation (National Oceanic and Atmospheric Administration, 2015). The initial drought may have promoted seedling establishment by lowering water tables (Roy et al., 2000). However, clearcuts and group selections showed simultaneous increases in densities of the shrub species, *Alnus incana* and *Acer spicatum,* which may form dense cover following harvesting (Harvey and Bergeron, 1989) and hinder future tree regeneration in the mechanical treatments.

4.2 Herbaceous community composition

Overstory treatment influenced both the height and composition of the herbaceous layer, with potential implications for tree seedling regeneration. Herbaceous layer height increased with decreasing overstory cover, which is consistent with the findings of Aubin et al. (2000) in southern boreal forests. Interception of available light, which is generally lower in the herbaceous layer than in the shrub layer, also increases as overstory cover

decreases (Aubin et al., 2000). In the clearcut, girdle, and group selection treatments, mean herbaceous layer height exceeded the height of the small and medium woody vegetation size classes in this study. Mean total herbaceous cover averaged over 200% in all treatments, which suggests that microsites where tree seedlings could escape herbaceous competition were rare.

Results of the PERMANOVA analysis for 2015 indicated herbaceous community composition responded to overstory treatments. The control and girdling treatment were not statistically different from one another. The ordination showed both the control and girdling treatment were associated with diverse communities of obligate and facultative wetland plants such as *Rubus pubescens, Geum rivale, Mitella nuda, Dryopteris carthusiana,* and *Equietum pratense.* These species are characteristic of closed, mesic forests in the region (Rogers et al., 2008). *Arisaema triphyllum* and *Asarum canadense* were also associated with the girdle and control treatments and are typical of undisturbed, wet-mesic hardwood sites (Jenkins and Parker, 2000). High spring water levels in *F. nigra* forests create seasonal pools (Palik and Kastendick, 2010), which support diverse plant communities yet contain few endemic species (Palik et al., 2007).

Water table rise in the girdle treatment (Slesak et al., 2014) was reflected in increased relative cover of wetland indicator species. The short-term effects of girdling were limited to overstory removal, since neither understory vegetation nor soil was disturbed. In the conceptual model of Roberts (2004), disturbances with effects confined to the overstory are expected to stimulate species with aboveground vegetative reproduction, as well as those with seeds stored in the soil seed bank. In agreement with

this model, we found the girdling treatment promoted two significant rhizomatous indicator species: the fern, *Matteuccia struthiopteris,* and the sedge, *Carex radiata.* Ferns may form dense layers which inhibit tree regeneration through a combination of shading, belowground competition, and allelopathy (George and Bazzaz, 1999). The significant girdling indicator species, *Arisaema triphyllum,* a shade-tolerant perennial characteristic of undisturbed wet/mesic forests (Jenkins and Parker, 2000), suggests shade from the herbaceous and woody vegetation layers has largely compensated for loss of the *F. nigra* overstory. The lower regeneration density of most tree species in this treatment may be linked to the dense herbaceous layer.

Group selections supported herbaceous communities that were compositionally intermediate of other treatments in both PERMANOVA and ordination analysis. Furthermore, we found no significant indicator species for this treatment. The lack of distinctive plant communities may reflect the sampling design, in which four of six sampling plots were located in harvested groups, while two plots were located in untreated matrix. Unfortunately, differences in sampling intensity within the group selection treatment prevented direct comparison between harvested groups and untreated matrix. However, a study of herbaceous communities following group selection harvest in Wisconsin found harvested groups supported greater abundances of disturbance-adapted species compared to untreated matrix (Shields and Webster, 2007). The relatively small 400m^2 size of the group openings likely also limited the duration of direct sunlight at the high latitude of the study area (Canham et al., 1990). A study in Michigan *Betula alleghaniensis* Britton forest found harvested groups had increased importance of

wetland indicator species, including *Arisaema triphyllum*, compared to untreated matrix (Shields and Webster, 2007). Palik and Kastendick (2010) found retaining a 15.3m buffer of partially harvested forest around *F. nigra* and *P. tremuloides*-dominated seasonal pools mitigates increases in graminoid cover associated with clearcutting.

Our results support previous research that found clearcuts are associated with high relative *Carex* spp. and other graminoid cover (Slesak et al., 2014), including the grass, *Calamagrostis canadensis*, a significant indicator species for this treatment in 2015, and the sedge, *Carex lacustris*. Clearcutting of *F. nigra/P. tremuloides*-dominated seasonal pools was also associated with increased graminoid importance in an earlier study (Palik and Kastendick, 2010). *Calamagrostis canadensis* has been associated with regeneration failures in boreal forests following harvesting (Lieffers et al., 1993). In addition to competition from living plants, matted dead *Calamagrostis canadensis* vegetation increases soil freezing, reducing the growing season for tree species and suppressing the suckering response of *P. tremuloides* (Lieffers et al., 1996). While both *Calamagrostis canadensis* and *Carex lacustris* are obligate wetland species (Lichvar et al., 2016), clearcutting did not lead to an overall increase in obligate wetland species cover as we had anticipated. In contrast to the findings of Klooster et al. (2012) in Michigan and Ohio mixed *Fraxinus* forests, invasive species were unimportant in our study area. We found low cover of the invasive forb, *Crepis tectorum*, which increased in all treatments in 2015. The invasive grass *Phalaris arundinacea* L. occurred sporadically in the clearcuts, but was too rare to be included in the multivariate analyses.

All treatments showed dramatic compositional changes between 2013 and 2015, indicative of increased species diversity and graminoid cover. A drought in 2012 (National Oceanic and Atmospheric Administration, 2015) likely influenced community composition in the following year. Reduced seasonal water levels may allow a greater variety of waterlogging-intolerant species to regenerate from the soil seedbank (Keddy and Reznicek, 1986). Changes in relative cover may also be more pronounced following drought's end, due to lagged effects on soil seedbanks (Stampfli and Zeiter, 2004). Greater 2012 water table rise in the clearcut treatments (Slesak et al., 2014) may have offset drought effects, rendering clearcut herbaceous communities more similar between sampling periods than other treatments.

5 Conclusions

Artificial regeneration in harvesting treatments, possibly combined with shrub and herbaceous layer control in EAB-girdled stands, may be necessary to restock *F. nigra* forests following EAB invasion. While *F. nigra* was the most abundant tree species, particularly in harvested areas, there is little likelihood this species could reach reproductive maturity before re-infestation in the event of heavy EAB invasion (Aubin et al., 2015). The second-most abundant species, *U. americana*, was widespread regardless of overstory treatment, but, while *U. americana* trees usually survive to reproductive age, they generally succumb to Dutch elm disease before reaching the overstory. *Quercus macrocarpa*, the third-most abundant species, had moderately high density in the control, clearcut, and group selection treatments, and could potentially aid in maintaining

overstory cover provided advance regeneration is protected during harvesting. While clearcutting promoted the highest density of non-EAB-host species, including *P. balsamifera, P. tremuloides,* and *U. americana,* the number of seedlings fell far short of recommended regeneration density for *F. nigra* stands (Erdmann et al., 1987).

Background variation in experimental blocks, likely reflecting differences in hydrology, appears to be the main influence on the woody vegetation community regardless of treatment. The pre-existing composition of the woody vegetation community, therefore, heavily influences post-disturbance patterns. Sites with lower abundance of shrub species and higher established tree regeneration should be prioritized for management activities. While harvesting treatments reduced shrub competition, additional shrub removal may be necessary to aid tree regeneration in stands affected by EAB.

Herbaceous layer height was greater in treatments with reduced overstory cover. Thus, herbaceous growth may inhibit tree regeneration to a greater degree in harvested treatments than in unharvested controls. The clearcut treatment also appeared to foster competition from graminoids, notably *Calamagrostis canadensis.* Herbaceous plant communities in the girdling treatment were more similar to those in controls than in clearcuts, suggesting EAB mortality may not introduce novel changes to herbaceous communities relative to historic management practices in the short term. However, the girdling treatment was associated with an increase in the fern layer, which may suppress tree regeneration in unmanaged stands following EAB invasion. Our results suggest tree

seedlings may require herbaceous competition control treatments under low canopy cover conditions.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx/doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. Can. J. For. Res. 30, 168–177. http://dx/doi.org/10.1139/x99-185.

Aubin, I., Cardou, F., Ryall, K., Kreutzweiser, D., Scarr, T., 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. For. Chron. 91, 291–298. http://dx/doi.org/10.5558/tfc2015-050.

Barnes, B.V., 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. Can. J. Bot. 54, 19–24. http://dx/doi.org/10.1139/b76-004.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw. 67, 1-48. http://dx.doi.org/10.18637/jss.v067.i01.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631. http://dx/doi.org/10.1139/x90-084.

Cowell, C.M., Hoalst-Pullen, N., Jackson, M.T., 2010. The limited role of canopy gaps in the successional dynamics of a mature mixed Quercus forest remnant. J. Veg. Sci. 21, 201–212. http://dx/doi.org/10.1111/j.1654-1103.2009.01137.x.

Dey, D.C., Jacobs, D., McNabb, K., Miller, G., Baldwin, V., Foster, G., 2008. Artificial regeneration of major oak (*Quercus*) species in the eastern United States—A review of the literature. For. Sci. 54, 77–106.

Doucet, R., 1989. Regeneration silviculture of aspen. For. Chron. 65, 23–27. http://dx/doi.org/10.5558/tfc65023-1.

Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486. http://dx/doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States, in: USDA Forest Service. ASDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115.

Flower C.E., Knight K.S., Gonzalez-Meler M.A., 2013. Impacts of the emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol. Invasions. 15, 931-944. http://dx/doi.org/10.1007/s10530-012-0341-7.

Gandhi, K.J., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions 12, 389–405. http://dx/doi.org/10.1007/s10886-009-9724-3.

George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. Ecology 80, 833–845. http://dx/doi.org/10.2307/177021.
Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57, 845–858. http://dx/doi.org/10.1641/B571007.
Hannah, P.R., 1988. The shelterwood method in northeastern forest types: A literature review. North. J. Appl. For. 5, 70–77.
Hannah, P.R., 1987. Regeneration methods for oaks. North. J. Appl. For. 4, 97–101.
Harvey, B.D., Bergeron, Y., 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. 19, 1458–1469. http://dx/doi.org/10.1139/x89-222.
Hausman, C.E., Jaeger, J.F., Rocha, O.J., 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. Biol. Invasions 12, 2013–2023. http://dx/doi.org/10.1007/s10530-009-9604-3.
Heinselman, M.L., 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz Region, Minnesota. Ecol. Monogr. 327–374.
Herms, D.A., McCullough, D.G., 2014. Emerald ash borer invasion of North America: History, biology, ecology, impacts and management. Annu. Rev. Entomol. 59, 13–30. http://dx/doi.org/10.1146/annurev-ento-011613-162051.
Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx/doi.org/10.1007/s10021-015-9929-y.
Jenkins, M.A., Parker, G.R., 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. Plant Ecol. 151, 223–237. http://dx/doi.org/10.1023/A:1026575219518.
Kashian, D.M., Witter, J.A., 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. For. Ecol. Manag. 261, 480–488. http://dx/doi.org/10.1016/j.foreco.2010.10.033
Keddy, P.A., MacLellan, P., 1990. Centrifugal organization in forests. Oikos 59, 75–84.
Keddy, P.A., Reznicek, A.A., 1986. Great Lakes Vegetation Dynamics: The role of fluctuating water levels and buried seeds. J. Gt. Lakes Res. 12, 25–36. http://dx/doi.org/10.1016/S0380-1330(86)71697-3.
Klooster, W.S., 2012. Forest Responses to Emerald Ash Borer-Induced Ash Mortality (Dissertation). Department of Horticulture and and Crop Science, The Ohio State University.
Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 16, 859–873. http://dx/doi.org/10.1007/s10530-013-0543-7.

Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29, 1–27.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. http://dx/doi.org/10.1046/j.1365-2435.2002.00664.x.
Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. 69, 1–33. http://dx/doi.org/10.18637/jss.v069.i01.
Lichvar, R.W., Banks, D.L., Kirchner, W.N., Melvin, N.C., 2016. The national wetland plant list: 2016 wetland ratings. Phytoneuron 30, 1–15. http://dx/doi.org/10.1016/j.foreco.2016.05.050.
Lieffers, V.J., Macdonald, S.E., Hogg, E.H., 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23, 2070–2077. http://dx/doi.org/10.1139/x93-258.
Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., Branter, K., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286–292. http://dx/doi.org/10.5558/tfc72286-3.
Looney, C.E., DAmato, A.W., Palik, B.J., Slesak, R., 2016. Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by emerald ash borer in Minnesota, USA. Can. J. For. Res. http://dx/doi.org/10.1139/cjfr-2016-0369.
Looney, C.E., D'Amato, A.W., Palik, B.J., Slesak, R.A., 2015. Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Can. J. For. Res. 45, 1728–1738. http://dx/doi.org/10.1139/cjfr-2015-0129.
McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
McCune, B., Medford, M., 2011. PC-ORD Version 6: Multivariate analysis of ecological data. MjM Software Design, Glendon Beach, OR.
McDonald, P.M., Abbott, C.S, 1994. Seedfall, regeneration, and seedling development in group-selection openings. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, Res. Paper PSW-RP-220.
Minnesota Wildflowers, 2016. https://www.minnesotawildflowers.info (accessed 8.22.16).
MNDNR, 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, MN.
National Oceanic and Atmospheric Administration, 2015. National Climatic Data Center: Minnesota Climate Division 2 http://www1.ncdc.noaa.gov/pub/data/cirs/ (accessed 7.10.15).
Native Plant Information Network, 2016. . Lady Bird Johns. Wildflower Cent. https://www.wildflower.org/explore/ (accessed 8.22.16).

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. http://dx/doi.org/10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.
Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front. Ecol. Environ. 3, 421–428. http://dx/doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.
Orwig, D., 2002. Ecosystem to regional impacts of introduced pests and pathogens: Historical context, questions and issues. J. Biogeogr. 29, 1471–1474. http://dx/doi.org/10.1046/j.1365-2699.2002.00787.x.
Palik, B.J., Streblow, D., Egeland, L., Buech, R., 2007. Landscape variation of seasonal pool plant communities in forests of northern Minnesota, USA. Wetlands 27, 12–23. http://dx/doi.org/10.1672/0277-5212(2007)27[12:LVOSPP]2.0.CO;2.
Palik, B.J., Kastendick, D., 2010. Response of seasonal pond plant communities to upland forest harvest in northern Minnesota forests, USA. For. Ecol. Manag. 260, 628–637. http://dx/doi.org/10.1016/j.foreco.2010.05.019.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. For. Ecol. Manag. 269, 26–30. http://dx/doi.org/10.1016/j.foreco.2011.12.020.
Peck, J., 2010. Multivariate anaylysis for community ecologists: step-by-step using PC-ORD. MjM Software Design, Gleneden Beach, OR.
Preisser, E.L., Oten, K.L.F., Hain, F.P., 2014. Hemlock woolly adelgid in the eastern United States: What have we learned? Southeast. Nat. 12, 1–15. http://dx/doi.org/ 10.1656/058.013.s604.
PRISM Climate Group, 2015. PRISM climate data: Recent years (Jan 1981-June 2014) Northwest Alliance Comput. Sci. Eng. http://www.prism.oregonstate.edu/recent/ (accessed 1.11.15).
R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. 82, 1273–1283. http://dx/doi.org/10.1139/b04-091.
Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89, 2482–2492. http://dx/doi.org/10.1890/07-1129.1.
Roy, V., Ruel, J.-C., Plamondon, A.P., 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. For. Ecol. Manag. 129, 253–267. http://dx/doi.org/10.1016/S0378-1127(99)00170-X.
Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. http://dx/doi.org/10.1139/x06-025.
Scott, G.A.J., 1995. Canada's Vegetation: A World Perspective. McGill-Queen's Press, Montreal, Quebec.

Shields, J.M., Webster, C.R., 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. Can. J. For. Res. 37, 1797–1807. http://dx/doi.org/10.1139/X07-052.
Shipley, B., Keddy, P.A., Moore, D.R.J., Lemky, K., 1989. Regeneration and establishment strategies of emergent macrophytes. J. Ecol. 77, 1093–1110. http://dx/doi.org/10.2307/2260825.
Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx/doi.org/10.1139/cjfr-2014-0111.
Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1996. The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley and Sons, New York, NY.
Soil Survey Staff, 2016. . USDA Nat. Resour. Conserv. Serv. http://www.nrcs.usda.gov /wps /portal/nrcs/detailfull/soils/home/?cid=nrcs142p2_053587 (accessed 9.30.16).
Stampfli, A., Zeiter, M., 2004. Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. J. Ecol. 92, 568–576. http://dx/doi.org/10.1111/j.0022-0477.2004.00900.x.
Tardif, J., Bergeron, Y., 1999. Population dynamics of *fraxinus nigra* in response to flood-level variations in northwestern Quebec. Ecol. Monogr. 69, 107–125. http://dx/doi.org/10.1890/0012-9615(1999)069[0107:PDOFNI]2.0.CO;2
Telander, A.C., Slesak, R.A., D'Amato, A.W., Palik, B.J., Brooks, K.N., Lenhart, C.F., 2015. Sap flow of black ash in wetland forests of northern Minnesota, USA: Hydrologic implications of tree mortality due to emerald ash borer. Agric. For. Meteorol. 206, 4–11. doi:10.1016/j.agrformet.2015.02.019
The PLANTS database, 2016. . USDA Nat. Resour. Conserv. Serv. http://plants.usda.gov (accessed 8.22.16).
Tredici, P.D., 2001. Sprouting in temperate trees: A morphological and ecological review. Bot. Rev. 67, 121–140. http://dx/doi.org/10.1007/BF02858075.
Waring, K.M., O'Hara, K.L., 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. For. Ecol. Manag. 209, 27–41. http://dx/doi.org/10.1016/j.foreco.2005.01.008.
Zasada, J.C., Viereck, L.A., Foote, M.J., Parkenson, R.H., Wolff, J.O., Lankford Jr., L.A., 1981. Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. For. Chron. 57, 57–65. http://dx/doi.org/10.5558/tfc57057-2.

Table 1. Mean density (stems ha^{-1}) of regeneration of woody species by treatment with potential to reach tree stature on *F. nigra* wetland forest study sites in northern Minnesota, USA.

	Treatment				
Species	Clearcut	Control	Girdle	Group	Species Mean
FRNI	19980 ± 3871a	5788 ± 2930c	1806 ± 675d	10625 ± 1203b	9549 ± 1209a
ULAM	1429 ± 555a	1062 ± 340a	1448 ± 444a	1260 ± 356a	1300 ± 147b
QUMA	337 ± 221ab	566 ± 275a	129 ± 129c	319 ± 161b	337 ± 71c
POBA	526 ± 399a	169 ± 129b	40 ± 30c	119 ± 84bc	213 ± 215d
TIAM	79 ± 79b	20 ± 13b	40 ± 21b	476 ± 432a	153 ± 154d
POTR	169 ± 136a	30 ± 21b	169 ± 111a	20 ± 20b	97 ± 31d
Treatment Total	22520 ± 4351a	7629 ± 3054bc	3631 ± 700c	12818 ± 1629b	
Other	38 ± 46	83 ± 77	25 ± 33	46 ± 153	

Note: Abbreviations are as follows: FRNI=*Fraxinus nigra,* ULAM=*Ulmus americana,* QUMA= *Quercus macrocarpa,* POBA=*Populus balsamifera,* POTR=*Populus tremuloides,* TIAM=*Tilia americana.* Means and standard errors are provided for each species. Results of Tukey's post-hoc comparisons for individual species across treatments (rows) are shown by the letters following each mean. Means with different letters are significantly different at the 95% confidence level. For the treatment x species interaction, pairwise comparisons of treatment are nested within each species. Treatment totals include the six common tree species and exclude species listed as Other. Other=*Acer rubrum, Acer negundo, Picea glauca,* and *Fraxinus pennsylvanica,* tree species not occurring on all 8 blocks and too rare to include in the analysis.

Table 2. Significant woody and herbaceous treatment indicator species on *F. nigra* forest study sites in northern Minnesota, USA.

Response	Treatment	Species	Indicator Value	Significance
Woody vegetation	Clearcut	*F. nigra* stump sprout clusters (>50 cm)	62.3	0.002
Woody vegetation	Clearcut	*F. nigra* single vegetative sprouts (>50cm)	66.0	0.001
Woody vegetation	Girdle	*Acer spicatum* (>50cm)	49.4	0.037
Woody vegetation	Group	*F. nigra* seed-origin stems (>50cm)	39.6	0.04
Herbaceous layer	Clearcut	*Calamagrostis canadensis*	50.4	0.001
Herbaceous layer	Control	*Geum rivale*	35.3	0.04
Herbaceous layer	Girdle	*Arisaema triphyllum*	52.3	0.01
Herbaceous layer	Girdle	*Carex radiata*	51.5	0.02
Herbaceous layer	Girdle	*Matteuccia struthiopteris*	39.6	0.04

Note: For woody vegetation, the origin (vegetative vs. seed) and size class are included. Potential indicator values ranged from 0 to 100, while the cutoff for significance was 0.05.

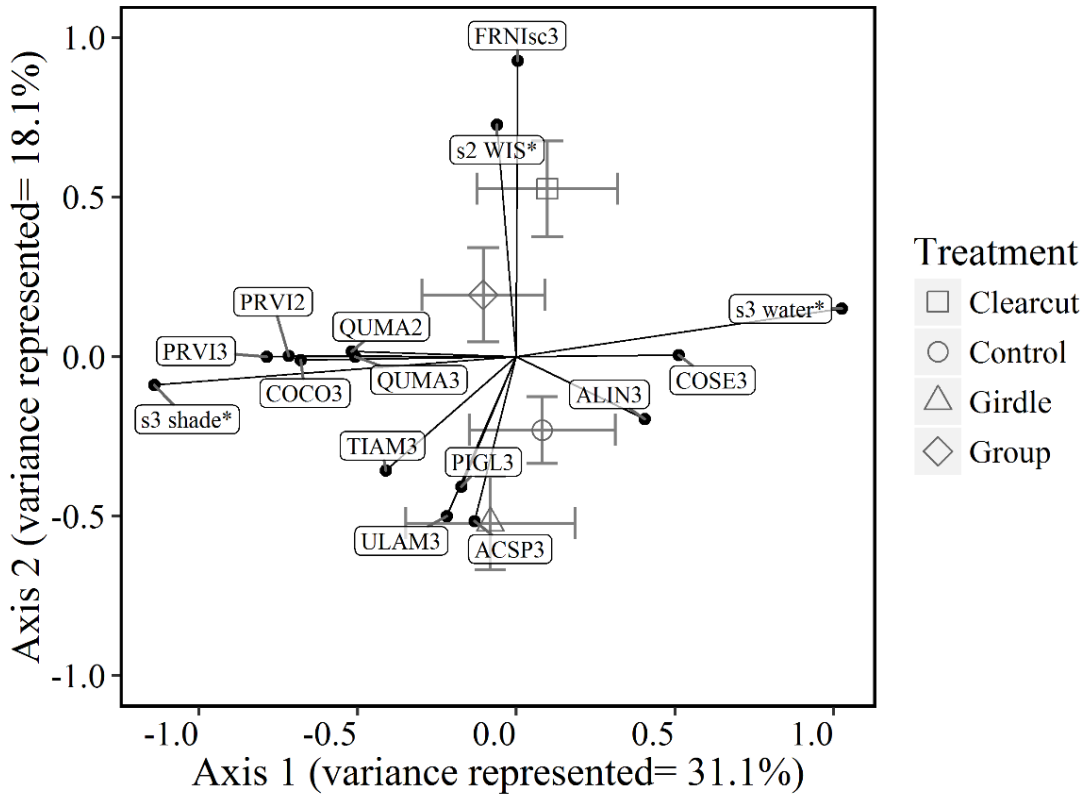

Figure 1. Ordination plot of woody vegetation community structure based on post-treatment data collected annually from 2012-2015. Overlays of mean treatment position (± S.E.) in species space are averaged over the 2012-2015 period. The first and second-most important axes of the three-dimensional ordination are shown. Individual species and explanatory variables are included in the biplot. The biplot displays the strength and direction of relationships with the ordination axes with a minimum r^2 of 0.20. Explanatory variables are designated by *. Numbers designate shoot size and origin: 1=small seedling, 2=medium seedling, 3=large seedling, s1=small single vegetative sprout, s2=medium single vegetative sprout, s3=large single vegetative sprout, sc1=small stump sprout cluster, sc2=medium stump sprout cluster, sc3=large stump sprout cluster. Abbreviations are as follows: WIS=wetland indicator status, COSE=Cornus sericea, water=waterlogging tolerance, ALIN=*Alnus incina,* QUMA=*Quercus macrocarpa,* PRVI= *Prunus viginiana,* COCO=*Corylus cornuta,* TIAM=*Tilia americana,* PIGL=*Picea glauca,* shade=shade tolerance.

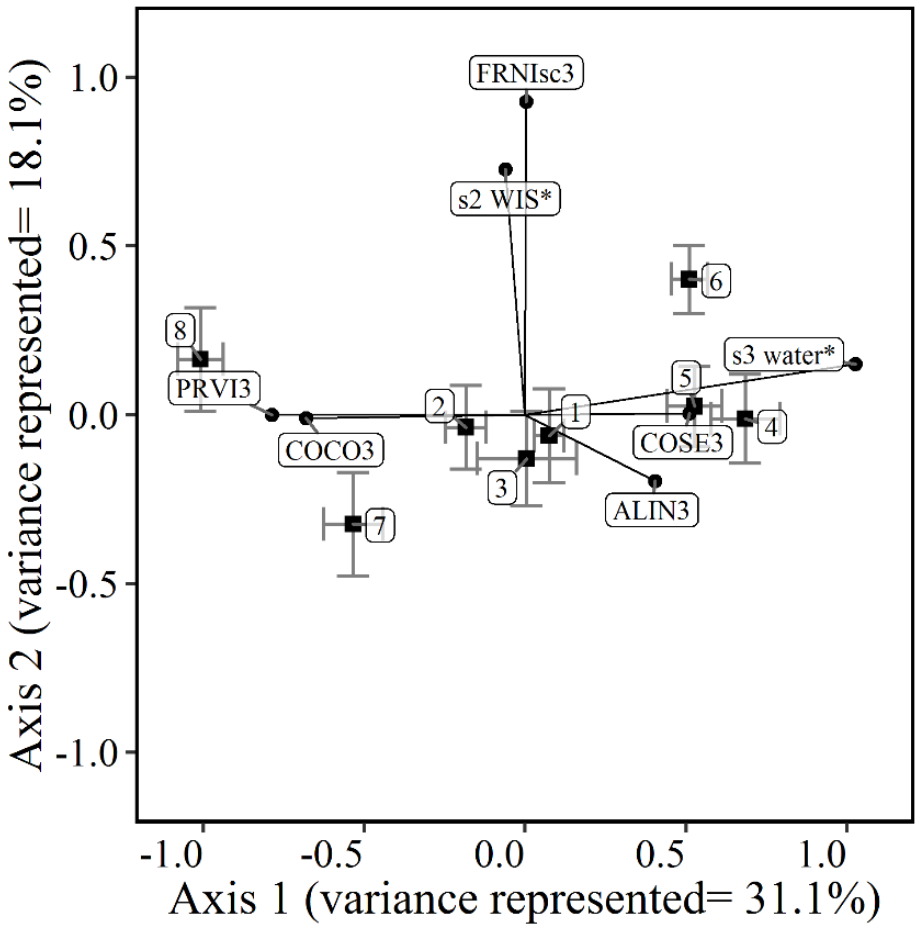

Figure 2. Ordination plot of woody vegetation community structure, showing mean block positions (± S.E.) in species space. Overlays of block positions are based on data averaged over the 2012-2015 post-treatment period. Numbers next to blocks (filled square symbols) correspond with block number. The first and second-most important axes of the three-dimensional ordination are shown. For clarity, only explanatory variables from Figure 1 (designated by *) are included in the biplot. The biplot displays the strength and direction of relationships with the ordination axes with a minimum r^2 of 0.20. Numbers adjacent to biplot variables (filled circle symbols) designate shoot size and origin: 1=small seedling, 2=medium seedling, 3=large seedling, s1=small single vegetative sprout, s2=medium single vegetative sprout, s3=large single vegetative sprout, sc1=small stump sprout cluster, sc2=medium stump sprout cluster, sc3=large stump sprout cluster. Abbreviations are as follows: FRNI=*Fraxinus nigra*, COSE=*Cornus sericea*, ALIN=*Alnus incana*, PRVI=*Prunus virginiana*, COCO=*Corylus cornuta*, WIS=wetland indicator status, water=waterlogging tolerance, shade=shade tolerance.

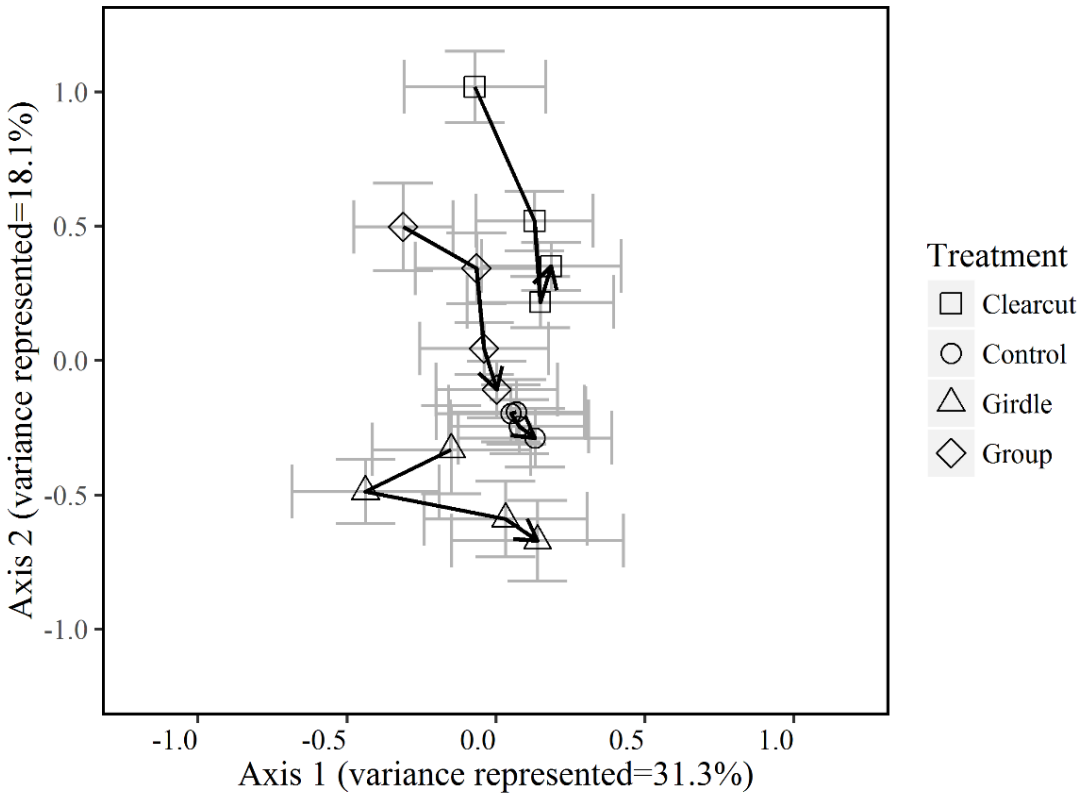

Figure 3. Ordination plot of woody vegetation community structure, showing successional trajectories of mean treatment positions in species space. Mean treatment positions (± S.E.) are provided for each year from 2012-2015. Arrows indicate successional trajectories showing the annual movement of treatments beginning in 2012 and ending in 2015. For all treatments, the oldest (2012) point is in the leftmost position of axis 1, while the most recent (2015) is in the rightmost portion. The first and second-most important axes of the three-dimensional ordination are shown.

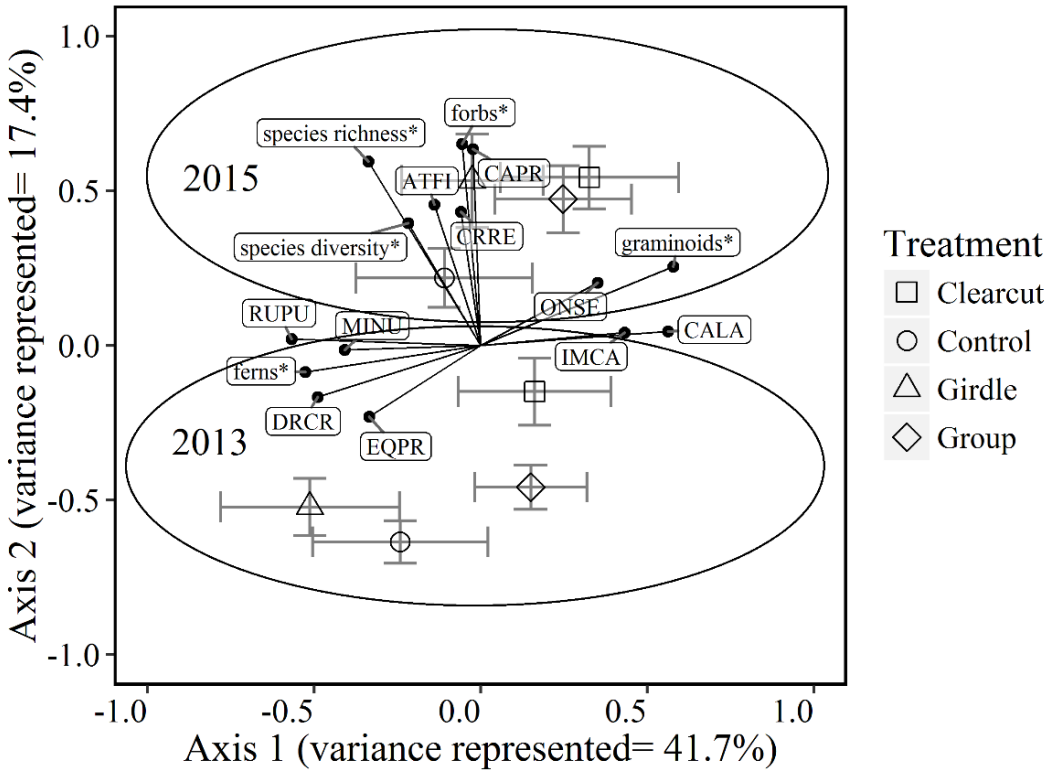

Figure 4. Ordination plot of herbaceous layer community structure, showing mean treatment positions (± S.E.) in species space for 2013 and 2015. The first and second most important axes of the three-dimensional ordination are shown. Individual species and explanatory variables are included in the biplot. The biplot displays the strength and direction of the relationship with the ordination axes of species with a minimum r^2 of 0.25. See text for additional, weaker relationships. * indicates explanatory variables. Abbreviations are as follows: ONSE=*Onoclea sensibilis*, CALA=*Carex lacustris*, IMCA=*Impatiens capensis*, EQPR= *Equisetum pratense*, DRMA=*Dryopteris carthusiana*, WIS=wetland indicator status, MINU=*Mitella nuda*, RUPU=*Rubus pubescens*, ATFI= *Athryium filix-femina*, CAPR= *Carex praegracilis*, CRTE= *Crepis tectorum*.

Chapter 6

Conclusions

1 Introduction

The overarching goal of this research was to extend the scientific basis for efforts to preserve forest cover and function in *Fraxinus nigra* Marsh. (black ash) wetland systems threatened by emerald ash borer (*Agrilus planipennis,* EAB). Toward this end, Chapter 2 assessed the influences of climate and competition on the growth of *F. nigra* in association with *Tilia americana* L. (basswood), *Populus tremuloides* Michx.(quaking aspen), and *Thuja occidentalis* L.(northern white-cedar) to better ascertain what limits these factors place on tree establishment at the drier and wetter *F. nigra* forest margins. Chapters 3 and 4 described the results of a field experiment that investigated the survival and growth of potential black ash replacement species planted under four canopy treatments for the purpose of identifying the most promising combinations of species and treatment for future EAB management efforts. Utilizing the treatment plots established for the planting experiment, Chapter 5 examined overstory treatment effects on established tree regeneration, as well as on the size and composition on the *F. nigra* forest shrub and herbaceous communities. Its goals were to determine the extent to which natural regeneration of associated tree species can be expected to contribute to forest cover and whether overstory treatment will aid or hinder this regeneration. The main findings of the four data chapters, together with their implications for management and future research, are discussed below.

2 Main findings

The Chapter 2 analysis of competition and climate effects found the growth of *F. nigra* did not vary across the topographic gradient of waterlogging stress, after correcting for the influences of competition and tree size. On the upland mesic and moist sites, *F. nigra* grew more slowly and appeared to be comparatively more sensitive to competition than *T. americana* and *P. tremuloides*, suggesting the two species may outcompete *F. nigra* at the drier margins of its habitat. On the wet bottomland sites, *F. nigra* showed slightly slower growth but appeared to have lower sensitivity to competition than *T. occidentalis*, indicating *T. occidentalis* may be more limited by competition than *F. nigra* on the hydric margins. For all species, competition appeared to be size-asymmetric, i.e., primarily for light. *Fraxinus nigra* growth responded positively to precipitation and negatively to temperature across the gradient of waterlogging stress. No growth-precipitation relationships were found for any of the associated tree species, suggesting mature trees (DBH $\geq$ 10 cm) of these species were relatively unaffected by moisture conditions at the study sites. Of the associated species, only *T. occidentalis* growth was negatively correlated with temperature. The growth-climate results suggest *F. nigra's* apparent sensitivity to drought may play a role in relegating the species to moderately hydric, bottomland sites.

Chapter 3 found overstory treatment and species combined to influence the survival of planted seedlings of potential *F. nigra* replacement tree species. The results suggest clearcutting, as in preemptive salvage logging, negatively impacted the survival

of 9 of 12 species tested, although unanticipated mechanical damage to seedlings during harvesting due to an unexpectedly low winter snowpack may have worsened survival in clearcuts and group selections. Nonetheless, control, group selection, and girdling treatments (which are emulative of planting just prior to EAB infestation) showed roughly equivalent seedling survival responses for the first several years. Planting season interacted with treatment to affect the survival of all species planted in both spring and fall, with the exception of *Celtis occidentalis* L. (hackberry) and *Populus deltoides* W. Bartram ex Marsh. (eastern cottonwood). Of the native species planted, *Ulmus americana* L. (American elm) had the highest survival rate, followed distantly by *Populus balsamifera* L. (balsam poplar) and *Acer rubrum* L. (red maple). Two species from the next southern climate zone, *Quercus bicolor* Willd. (swamp white oak) and *C. occidentalis,* had survival rates superior to those of all naturally occurring species examined, with the exception of *U. americana.*

As reported in Chapter 4, treatment and species also combined to influence planted seedling mean height and diameter relative growth rate (RGR). RGR generally decreased with increases in the overstory leaf area index (LAI), which measured 11%, 69%, and 82% of LAI in the control treatment in the clearcut, girdling, and group selection treatments, respectively. The clearcut treatment, which had lowest overall survival, promoted the most rapid mean RGR, especially of shade-intolerant species, followed by the girdle, group selection, and control. Shade-intolerant species that had moderate to low survival, such as *P. balsamifera, P. deltoides,* and *Larix laricina* (Du Roi) K. Koch. (tamarack), showed the highest RGR of all species across treatments. In

contrast, high surviving shade-tolerant species, such as *U. americana* and *C. occidentalis*, had among the lowest RGR. Species showing the most favorable balance of survival and growth included *Q. bicolor* and *P. balsamifera* in all treatments; *A. rubrum* in the control, girdle, and group selection treatments; and *U. americana* in the clearcut and girdle treatments.

The Chapter 5 analysis of groundlayer vegetation response to EAB and management strategies found *F. nigra* had the most abundant established regeneration of all tree species in all treatments. Among non-*Fraxinus* tree species, *U. americana,* had the most abundant established regeneration, followed by *Quercus macrocarpa* Michx. (bur oak), *P. balsamifera, T. americana*, and *P. tremuloides*. Combined regeneration density for non-*Fraxinus* species fell short of *F. nigra* forest stocking guidelines (Erdmann et al., 1987). In general, clearcutting promoted the highest density of both *F. nigra* and associated tree species, while girdling appeared to foster a combination of gradually increasing overstory light and rising water tables that resulted in depressed natural tree regeneration relative to undisturbed controls. While composition of the overall woody vegetation community also shifted in response to silvicultural treatments, background differences between blocks, likely related to site hydrology, appeared to account for approximately twice as much variation. The lower LAI of the clearcut and girdling treatments promoted increased herbaceous layer height, with the clearcut treatment shifting toward greater abundance of graminoids and the girdling treatment shifting toward greater abundance of ferns. In contrast to previous studies, no significant increase in invasive plant species was observed in response to changes in the overstory.

3 Management Recommendations

Chapter 2 found that mature *T. americana* and *P. tremuloides* appear well-suited in terms of both competition and climate to the mesic and moist topographic margins of the *F. nigra* forests we studied. Mature *T. occidentalis* appears only slightly less well-suited to the very wet margins. However, the co-occurrence of *F. nigra* with *T. americana* and *P. tremuloides* on the mesic and moist sites, despite *F. nigra*'s relatively slower growth and greater sensitivity to competition, suggests interspecific differences in natural regeneration success may play a role in the persistence of *F. nigra* at these sites. These differences should be investigated given their potential importance to the outcome of artificial regeneration efforts.

The results of the field experiment indicate that seedling plantings, with or without overstory treatment, may represent an effective strategy for establishing *F. nigra* replacement tree species as EAB approaches. Species selection will be critical to the success of any future planting efforts, with conifer and shade-intolerant hardwood species showing generally low survival rates. The relative success of angiosperm species over conifers should help managers avoid the more dramatic alterations to light, microclimate, and nutrient dynamics associated with conversion of hardwood to coniferous systems (Ford et al., 2012). While planting in controls resulted in high survival, it appears unviable for long-term growth in the absence of some disturbance. However, results for the girdling treatments suggest planting immediately prior to EAB invasion may support relatively high growth and survival for a variety of species. Group selection was

generally less effective than girdling in promoting growth, but could potentially offset planting costs through timber sales while supporting higher survival than the clearcut treatment. To take advantage of timber markets, treatments should be applied before EAB-invasion, given the likelihood of quarantines on timber from affected areas. While damage resulting from unusually low snow cover during winter harvesting may have reduced the overall effectiveness of fall plantings, the results nevertheless suggest that planting season should be determined by species to assure the greatest chance of seedling survival.

When projected shifts in suitable habitat due to warming climate are also considered, the combined survival and RGR results suggest that *A. rubrum, Q. bicolor,* and *U. americana* may be viable *F. nigra* replacement species under both present and future conditions (Iverson et al., 2008). In terms of both growth and survival, *Q. bicolor* appears to be a good candidate for assisted range expansion (Pedlar et al., 2012), although its fecundity in the study area should be monitored when it reaches reproductive potential. For *U. americana,* it must be noted that, even if Dutch elm disease-tolerant stock is used, there is a risk the disease could overcome tolerance (Slavicek and Knight, 2012). A fourth species, *P. balsamifera,* also achieved moderate survival and RGR but likely represents only a near-term solution if the climate continues to warm (Iverson et al., 2016). Species selection and treatment should be coordinated, with *Q. bicolor* and *P. balsamifera* suitable for planting under all overstory management scenarios; *A. rubrum* under group selection treatment and in untreated forest either prior to or at the approach

of EAB invasion; and *U. americana* in clearcut treatments and in untreated forest when EAB invasion is imminent.

While management strategies that rely on natural regeneration would involve lower immediate costs, low established regeneration of non-*Fraxinus* tree species suggests natural regeneration alone will be insufficient to mitigate loss of forest cover following EAB invasion. Although established regeneration of *F. nigra* was abundant regardless of overstory condition, particularly in the harvested areas, there is little likelihood this species could reach reproductive maturity before re-infestation in the event of heavy EAB invasion (Aubin et al., 2015). *Ulmus americana,* the non-*Fraxinus* species with the most abundant established regeneration, was similarly widespread; however, while *U. americana* trees usually survive to reproductive age, they generally succumb to Dutch elm disease before reaching the overstory. *Quercus macrocarpa,* the third-most abundant species, could potentially aid in maintaining overstory cover providing advance regeneration is protected during harvesting. It should be noted, however, that even in the clearcuts, which promoted the highest established regeneration density of non-*Fraxinus* species, established regeneration of all tree species combined fell short of stocking recommendations for *F. nigra* stands (Erdmann et al., 1987). Thus, artificial regeneration will be necessary to restock *F. nigra* forests following EAB invasion. Furthermore, although harvesting appears preferable to lack of management for promoting natural tree regeneration, depressed survival of planted seedlings in clearcuts suggests the same overstory management strategy may not be effective in promoting the growth of both naturally occurring and planted tree seedlings.

Overstory management also influenced woody shrub and herbaceous plant communities. However, background variation in experimental blocks, likely reflecting differences in hydrology, appeared to be the main influence on the woody shrub community. Thus, the pre-existing composition of the woody shrub community will heavily influence post-disturbance patterns. Drier sites generally appeared to foster higher advance tree regeneration and lower densities of competing shrubs regardless of overstory treatment. Prioritizing these sites for management may be more efficient than attempts to restore wetter, shrub-dominated sites. Girdling, as occurs with EAB invasion, appeared to promote an increase in both wetland shrub species and the fern layer, while harvesting promoted herbaceous layer growth, all of which may suppress tree regeneration by shading seedlings from light and creating unfavorable microsites for tree regeneration. These results suggest tree seedlings will require shrub and herbaceous competition control treatments under disturbed canopy conditions. While invasive species were not important in this study, previous research documented increases in invasive plants following EAB invasion (Klooster, 2012), suggesting future monitoring is warranted.

4 Future Research

The planting experiment was limited in its geographic scope, given the wide distribution of *F. nigra* in the Great Lakes region. Therefore, it is unclear how regeneration success may vary with geographic location. In addition, the study sites were largely located in physiographically similar, moderately wet stands at the center of *F.*

nigra's habitat, while associated species such as *P. tremuloides* and *T. americana* were found to be competitively and climatically well suited to the more mesic margins of *F. nigra* forests. Given the very low planted seedling survivorship of *P. tremuloides*, the use of natural microtopography or creation of somewhat drier establishment sites, e.g., through mounding, should be explored to minimize waterlogging stress and better insure the establishment of planted seedlings.

Given the low overall survival of seedlings only two years post-planting, research is needed into additional measures to improve seedling success and, thereby, the cost-effectiveness of artificial regeneration. The more robust seedling stock of high-surviving species such as *U. americana, Q. bicolor,* and *F. mandshurica* suggests future planting efforts should prioritize stock quality and matching stock characteristics to site (Landis et al., 2010). In the present study, a single stock type of each species was planted, whereas small preliminary plantings that test the survival of seedlings from several stock types per species might aid in better matching stock attributes with local site requirements (Landis et al. 2010).

Control of competition from the herbaceous understory and shrub layer, which was not implemented in the present study, is also a logical avenue for future research. As a starting point, follow-on research should evaluate the survival and growth response of both planted and naturally occurring seedlings to release from groundlayer competition. Although suppression of both artificial and natural tree regeneration from competing vegetation can be inferred from the results, formal removal experiments are necessary to establish a more rigorous causal relationship in *F. nigra* forests.

Finally, while not addressed in this dissertation, Great Lakes forests come under intense pressure from white-tailed deer (*Odocoileus virginianus*) browse (Rooney and Waller, 2003), which is expected to increase if warming climate reduces winter deer mortality (Fisichelli et al., 2012). While field data that showed evidence of deer browse, no measures were taken in the current study to protect seedlings from browse damage. Future research should quantify deer-browse damage to seedlings, and if extensive, evaluate the potential of deer fences or individual seedling protectors to improve survival and growth. Deer exclosures would also be useful for assessing the extent to which browse pressure may affect natural tree regeneration and herbaceous community composition in *F. nigra* wetland forests.

References

Aubin, I., Cardou, F., Ryall, K., Kreutzweiser, D., Scarr, T., 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. For. Chron. 91, 291–298. http://dx.doi.org/10.5558/tfc2015-050.

Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115.

Fisichelli, N.A., Frelich, L.E., Reich, P.B., Eisenhauer, N., 2012. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biol. Invasions 15, 1057–1066. http://dx.doi.org/10.1007/s10530-012-0350-6.

Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., Vose, J.M., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos 121, 523–536. http://dx.doi.org /10.1111/j.1600-0706.2011.19622.x.

Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx.doi.org /10.1007/s10021-015-9929-y.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manag., Forest landscape modeling - Approaches and applications 254, 390–406. http://dx.doi.org 10.1016/j.foreco.2007.07.023.

Klooster, W.S., 2012. Forest Responses to Emerald Ash Borer-Induced Ash Mortality (Ph.D. dissertation). Department of Horticulture and and Crop Science, The Ohio State University, Columbus, OH.

Landis, T.D., Dumroese, R.K., Haase, D.L., 2010. The Container Nursery Manual, Volume Seven: Seedling Processing, Storage and Outplanting. USDA Forest Service, Agricultural Handbook 674, Washington D.C.

Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. BioScience 62, 835–842. http://dx.doi.org /10.1525/bio.2012.62.9.10.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manag., Forest Dynamics and Ungulate Herbivory : From Leaf to Landscape 181, 165–176. http://dx.doi.org 10.1016/S0378-1127(03)00130-0.

Slavicek, J.M., Knight, K.S., 2012. Generation of American elm trees with tolerance to Dutch elm disease through controlled crosses and selection., in: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel, S.J. (Eds.), Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. Pacific

Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, CA, Gen. Tech. Rep. PSW-GTR-240, pp. 342–346.
Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx.doi.org /10.1139/cjfr-2014-0111.

Bibliography

Aakala, T., Fraver, S., D'Amato, A.W., Palik, B.J., 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. For. Ecol. Manag. 308, 128–135. http://dx/doi.org/10.1016/j.foreco.2013.07.057.

Abrams, M.D., 1998. The red maple paradox. BioScience 48, 355–364. http://dx/doi.org/10.2307/1313374.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. http://dx/doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest, Quebec. Can. J. For. Res. 30, 168–177. http://dx/doi.org/10.1139/x99-185.

Aubin, I., Cardou, F., Ryall, K., Kreutzweiser, D., Scarr, T., 2015. Ash regeneration capacity after emerald ash borer (EAB) outbreaks: Some early results. For. Chron. 91, 291–298. http://dx/doi.org/10.5558/tfc2015-050.

Aussenac, G., 2000. Interactions between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Ann. For. Sci. 57, 287–301. doi:10.1051/forest:2000119.

Barn http://dx/doi.org/es, B.V., 1976. Succession in deciduous swamp communities of southeastern Michigan formerly dominated by American elm. Can. J. Bot. 54, 19–24. doi:10.1139/b76-004

Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting Linear Mixed-Effects Models using lme4. J. Stat. Softw., 67, 1-48. http://dx.doi.org/10.18637/jss.v067.i01.

Benedict, M.A., Frelich, L.E., 2008. Site factors affecting black ash ring growth in northern Minnesota. For. Ecol. Manag. 255, 3489–3493. http://dx/doi.org/10.1016/j.foreco.2008.02.029.

Bergsten, U., Goulet, F., Lundmark, T., Löfvenius, M.O., 2001. Frost heaving in a boreal soil in relation to soil scarification and snow cover. Can. J. For. Res. 31, 1084–1092. http://dx/doi.org/10.1139/x01-042.

Binkley, D., Kashian, D.M., Boyden, S., Kaye, M.W., Bradford, J.B., Arthur, M.A., Fornwalt, P.J., Ryan, M.G., 2006. Patterns of growth dominance in forests of the Rocky Mountains, USA. For. Ecol. Manag. 236, 193–201. http://dx/doi.org/10.1016/j.foreco.2006.09.001.

Bunn, A.G., 2008. A dendrochronology program library in R (dplR). Dendrochronologia 26, 115–124. http://dx/doi.org/10.1016/j.dendro.2008.01.002.

Burnham, K.P., Anderson, D.R., 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Springer-Verlag, New York, NY.

Callaway, R.M., 2007. Interaction between Competition and Facilitation, in: Positive Interactions and Interdependence in Plant Communities. Springer, Dordrecht, The Netherlands, pp. 179–254.

Callaway, R.M., Pugnaire, F.I., 2007. Facilitation in plant communities, in: Pugnaire,

F.I., Valladeres, F. (Eds.), Functional Plant Ecology. CRC Press, Boca Raton, FL, pp. 435–453.
Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Can. J. For. Res. 20, 620–631. http://dx/doi.org/10.1139/x90-084.
Chen, H., 1997. Interspecific responses of planted seedlings to light availability in interior British Columbia: survival, growth, allometric patterns, and specific leaf area. Can. J. For. Res. 27, 1383–1393. http://dx/doi.org/10.1139/x97-099.
Chen, X., Chen, Z., 1999. Frost injury in Manchurian ash plantations. J. Northeast For. 27, 10–14.
Chojnacky, D., Rogers, P.C., 1999. Converting tree diameter at root collar (drc) to diameter at breast height (dbh). West. J. Appl. For. 14, 14–16.
Christersson, L., von Fircks, H.A., 1988. Injuries to conifer seedlings caused by simulated summer frost and winter desiccation. Silva Fenica 22, 195–201. http://dx/doi.org/ 10.14214/sf.
Coates, K.D., Canham, C.D., LePage, P.T., 2009. Above- versus below-ground competitive effects and responses of a guild of temperate tree species. J. Ecol. 97, 118–130. http://dx/doi.org/ 10.1111/j.1365-2745.2008.01458.x
Cohen, J.G., Kost, M.A., Slaughter, B.S., Albert, D.A., 2014. A Field Guide to the Natural Communities of Michigan. Michigan State University Press, East Lansing, MI.
Cole, W.G., Lorimer, C.G., 1994. Predicting tree growth from crown variables in managed northern hardwood stands. For. Ecol. Manag. 67, 159–175. http://dx/doi.org/10.1016/0378-1127(94)90014-0
Coomes, D.A., Allen, R.B., 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95, 1084–1097. http://dx/doi.org/ 10.1111/j.1365-2745.2007.01280.x
Cowell, C.M., Hoalst-Pullen, N., Jackson, M.T., 2010. The limited role of canopy gaps in the successional dynamics of a mature mixed Quercus forest remnant. J. Veg. Sci. 21, 201–212. http://dx/doi.org/ 10.1111/j.1654-1103.2009.01137.x
Cumming, S.G., Schmiegelow, F.K.A., Burton, P.J., 2000. Gap dynamics in boreal aspen stands: Is the forest older than we think. Ecol. Appl. 10, 744–759. http://dx/doi.org/ 10.2307/2641042.
DeSantis, R.D., Moser, W.K., Gormanson, D.D., Bartlett, M.G., Vermunt, B., 2013. Effects of climate on emerald ash borer mortality and the potential for ash survival in North America. Agric. For. Meteorol., Special Issue:Drought Inner Asia 178–179, 120–128. http://dx/doi.org/ 10.1016/j.agrformet.2013.04.015.
Dey, D.C., Jacobs, D., McNabb, K., Miller, G., Baldwin, V., Foster, G., 2008. Artificial regeneration of major oak (*Quercus*) species in the eastern United States—A review of the literature. For. Sci. 54, 77–106.
Dix, M.E., Buford, M., Slavicek, J.M., Solomon, A.M., Conrad, S.G., 2010. Invasive species and disturbances: Current and future roles of Forest Service research and development, in: A Dynamic Invasive Species Research Vision: Opportunities and Priorities 2009-29. pp. 91–102. https://www.fs.fed.us/research/docs/invasive-

species/wo_gtr79_83/ wo_ gtr79_ 83_091.pdf (accessed 12.2.2014).
Dixon, G.E., Keyser, C.E., 2008. Lake States (LS) Variant Overview: Forest Vegetation Simulator, Internal Rep. USDA Forest Service, Forest Management Service Center, Fort Collins, CO.
Doucet, R., 1989. Regeneration silviculture of aspen. For. Chron. 65, 23–27. http://dx.doi.org/10.5558/tfc65023-1
Dudek, D.M., McClenahen, J.R., Mitsch, W.J., 1998. Tree growth responses of *Populus deltoides* and *Juglans nigra* to streamflow and climate in a bottomland hardwood forest in central Ohio. Am. Midl. Nat. 140, 233–244http://dx/doi.org/10.1674/0003-0031(1998)140[0233:TGROPD]2.0.CO;2
Dulohery, C.J., Kolka, R.K., McKevlin, M.R., 2000. Effects of a willow overstory on planted seedlings in a bottomland restoration. Ecol. Eng. 15, S57–S56. doi:10.1016/S0925-8574(99)00072-5
Dymond, S.F., D'Amato, A.W., Kolka, R.K., Bolstad, P.V., Sebestyen, S.D., Bradford, J.B., 2015. Growth-climate relationships across topographic gradients in the northern Great Lakes. Ecohydrology. http://dx/doi.org/10.1002/eco.1700.
Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front. Ecol. Environ. 3, 479–486. http://dx/doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2
Epstein, E.J., Judziewicz, E.J., Spencer, E.A., 2002. Northern Hardwood Swamp, in: Wisconsin Natural Community Abstracts. Department of Natural Resources, Bureau of Endangered Resources, Madison, WI.
Erdmann, G.G., Crow, T.R., Peterson Jr, R.M., Wilson, C.D., 1987. Managing black ash in the Lake States. USDA Forest Service, North Central Forest Experimental Station, St. Paul, MN, Gen. Tech. Rep. NC-115.
Fassnacht, K.S., Gower, S.T., 1997. Interrelationships among the edaphic and stand characteristics, leaf area index, and aboveground net primary production of upland forest ecosystems in north central Wisconsin. Can. J. For. Res. 27, 1058–1067. http://dx/doi.org/ 10.1139/x97-058.
Fisichelli, N.A., Frelich, L.E., Reich, P.B., Eisenhauer, N., 2012. Linking direct and indirect pathways mediating earthworms, deer, and understory composition in Great Lakes forests. Biol. Invasions 15, 1057–1066. http://dx/doi.org/10.1007/s10530-012-0350-6.
Flower, C.E., Knight, K.S., Gonzalez-Meler, M.A., 2013. Impacts of the emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol. Invasions 15, 931–944. http://dx/doi.org/10.1007/s10530-012-0341-7.
Ford, C.R., Elliott, K.J., Clinton, B.D., Kloeppel, B.D., Vose, J.M., 2012. Forest dynamics following eastern hemlock mortality in the southern Appalachians. Oikos 121, 523–536. http://dx/doi.org/10.1111/j.1600-0706.2011.19622.x.
Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version

2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser Univ. Burnaby Br. Columbia Inst. Ecosyst. Stud., Millbrook. N. Y.
Frelich, L.E., 2002. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests. Cambridge University Press, Cambridge, UK.
Frey, B.R., Lieffers, V.J., Hogg, E. (Ted), Landhäusser, S.M., 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. Can. J. For. Res. 34, 1379–1390. http://dx/doi.org/10.1139/x04-062.
Galatowitsch, S., Frelich, L., Phillips-Mao, L., 2009. Regional climate change adaptation strategies for biodiversity conservation in a midcontinental region of North America. Biol. Conserv. 142, 2012–2022. http://dx/doi.org/10.1016/j.biocon.2009.03.030.
Gandhi, K.J., Herms, D.A., 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol. Invasions 12, 389–405. http://dx/doi.org/10.1007/s10886-009-9724-3.
George, L.O., Bazzaz, F.A., 1999. The fern understory as an ecological filter: Emergence and establishment of canopy-tree seedlings. Ecology 80, 833–845. http://dx/doi.org/10.2307/177021
Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57, 845–858. http://dx/doi.org/10.1641/B571007.
Girardin, M.-P., Tardif, J., Bergeron, Y., 2001. Radial growth analysis of *Larix laricina* from the Lake Duparquet area, Québec, in relation to climate and larch sawfly outbreaks. Écoscience 8, 127–138. http://dx/doi.org/10.1080/11956860.2001.11682638.
Goulet, F., 1995. Frost heaving of forest tree seedlings: a review. New For. 9, 67–94. http://dx/doi.org/10.1007/BF00028927.
Gucker, C.L., 2005. *Fraxinus nigra*. Fire Eff. Syst. http://www.fs.fed.us/database/feis (accessed 6.10.15).
Hannah, P.R., 1988. The shelterwood method in northeastern forest types: A literature review. North. J. Appl. For. 5, 70–77.
Hannah, P.R., 1987. Regeneration methods for oaks. North. J. Appl. For. 4, 97–101.
Hansen, E.A., 1986. Planting date affects survival and height growth of hybrid poplar. For. Chron. 62, 164–169. http://dx/doi.org/10.5558/tfc62164-3.
Harvey, B.D., Bergeron, Y., 1989. Site patterns of natural regeneration following clear-cutting in northwestern Quebec. Can. J. For. Res. 19, 1458–1469. http://dx/doi.org/10.1139/x89-222.
Hausman, C.E., Jaeger, J.F., Rocha, O.J., 2010. Impacts of the emerald ash borer (EAB) eradication and tree mortality: potential for a secondary spread of invasive plant species. Biol. Invasions 12, 2013–2023. http://dx/doi.org/10.1007/s10530-009-9604-3.
Heinselman, M.L., 1963. Forest sites, bog processes, and peatland types in the Glacial Lake Agassiz Region, Minnesota. Ecol. Monogr. 327–374. http://dx/doi.org/10.2307/1950750.
Herms, D.A., McCullough, D.G., 2014a. Emerald ash borer invasion of North America:

History, biology, ecology, impacts and management. Annu. Rev. Entomol. 59, 13–30. http://dx/doi.org/10.1146/annurev-ento-011613-162051.
Herms, D.A., McCullough, D.G., 2014b. Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. Annu. Rev. Entomol. 59, 13–30. http://dx/doi.org/10.1146/annurev-ento-011613-162051
Hofmeyer, P.V., Kenefic, L.S., Seymour, R.S., 2009a. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: A synthesis of knowledge. North. J. Appl. For. 26, 21–27.
Hofmeyer, P.V., Seymour, R.S., Kenefic, L.S., 2009b. Influence of soil site class on growth and decay of northern white-cedar and two associates in Maine. North. J. Appl. For. 26, 68–75.
Holmes, R.L., 1983. Computer-assisted quality control in tree-ring dating and measurement. Tree-Ring Bull. 43, 69–78.
Houle, G., Bouchard, F., 1990. Hackberry (*Celtis occidentalis*) at the northeastern limit of its distribution in North America: population structure and radial growth patterns. Can. J. Bot. 68, 2685–2692. http://dx/doi.org/10.1139/b90-339.
Hunt, R., Cornelissen, J.H.C., 1997. Components of relative growth rate and their interrelations in 59 temperate plant species. New Phytol. 135, 395–417. http://dx/doi.org/10.1046/j.1469-8137.1997.00671.x.
Iverson, L., Knight, K.S., Prasad, A., Herms, D.A., Matthews, S., Peters, M., Smith, A., Hartzler, D.M., Long, R., Almendinger, J., 2016. Potential species replacements for black ash (*Fraxinus nigra*) at the confluence of two threats: Emerald ash borer and a changing climate. Ecosystems 19, 248–270. http://dx/doi.org/10.1007/s10021-015-9929-y.
Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manag., Forest landscape modeling - Approaches and applications 254, 390–406. http://dx/doi.org/10.1016/ j.foreco.2007.07.023.
Jack, S.B., Long, J.N., 1996. Linkages between silviculture and ecology: an analysis of density management diagrams. For. Ecol. Manag. 86, 205–220. http://dx/doi.org/10.1016/S0378-1127(96)03770-X.
Jean, M., Bouchard, A., 1996. Tree-ring analysis of wetlands of the upper St. Lawrence River, Quebec: response to hydrology and climate. Can. J. For. Res. 26, 482–491. http://dx/doi.org/ 10.1139/x26-054.
Jenkins, M.A., Parker, G.R., 2000. The response of herbaceous-layer vegetation to anthropogenic disturbance in intermittent stream bottomland forests of southern Indiana, USA. Plant Ecol. 151, 223–237. http://dx/doi.org/10.1023/ A:1026575219518.
Jobidon, R., Charette, L., Bernier, P.Y., 1998. Initial size and competing vegetation effects on water stress and growth of *Picea mariana* (Mill.) BSP seedlings planted in three different environments. For. Ecol. Manag. 103, 293–305. http://dx/doi.org/10.1016/S0378-1127(97)00228-4.
Jonckheere, I., Fleck, S., Nackaerts, K., Muys, B., Coppin, P., Weiss, M., Baret, F., 2004.

Review of methods for in situ leaf area index determination: Part I. Theories, sensors and hemispherical photography. Agric. For. Meteorol. 121, 19–35. http://dx/doi.org/ 10.1016/j.agrformet.2003.08.027.
Jones, R.H., Sharitz, R.R., 1998. Survival and growth of woody plant seedlings in the understorey of floodplain forests in South Carolina. J. Ecol. 86, 574–587. http://dx/doi.org/ 10.1046/j.1365-2745.1998.00287.x.
Kabrick, J.M., Dey, D.C., Van Sambeek, J.W., Coggeshall, M.V., Jacobs, D.F., 2012. Quantifying flooding effects on hardwood seedling survival and growth for bottomland restoration. New For. 43, 695–710. http://dx/doi.org/10:1007/s11056-012-9331-y.
Kashian, D.M., Witter, J.A., 2011. Assessing the potential for ash canopy tree replacement via current regeneration following emerald ash borer-caused mortality on southeastern Michigan landscapes. For. Ecol. Manag. 261, 480–488. http://dx/doi.org/10.1016/j.foreco.2010.10.033.
Keddy, P.A., 2001. Competition Gradients, in: Competition, Population, and Community Ecology. Springer, Dordrecht, The Netherlands, pp. 281–315.
Keddy, P.A., MacLellan, P., 1990. Centrifugal organization in forests. Oikos 59, 75–84. http://dx/doi.org/10.2307/3545125.
Keddy, P.A., Reznicek, A.A., 1986. Great Lakes vegetation dynamics: The role of fluctuating water levels and buried seeds. J. Gt. Lakes Res. 12, 25–36. http://dx/doi.org/ 10.1016/S0380-1330(86)71697-3.
Klooster, W.S., 2012. Forest Responses to Emerald Ash Borer-Induced Ash Mortality (Ph.D. dissertation). Department of Horticulture and Crop Science, The Ohio State University, Columbus, OH.
Klooster, W.S., Herms, D.A., Knight, K.S., Herms, C.P., McCullough, D.G., Smith, A., Gandhi, K.J.K., Cardina, J., 2014. Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol. Invasions 16, 859–873. http://dx/doi.org/10.1007/s10530-013-0543-7.
Knight, K.S., Herms, D.A., Cardina, J., Long, R., Rebbeck, J., Gandhi, K.J., Smith, A., Klooster, W.S., Herms, C.P., Royo, A.A., 2010. Emerald ash borer aftermath forests: the dynamics of ash mortality and the responses of other plant species: Notes, in: Michler, C.H., Ginzel, M.D. (Eds.), Proceedings of Symposium on Ash in North America. USDA Forest Service, Northern Research Station, Newton Square, PA, Gen. Tech. Rep. NRS P-72, p. 11.
Knight, K.S., Slavicek, J.M., Kappler, R., Pisarczyk, E., Wiggin, B., Menard, K., 2012. Using Dutch elm disease-tolerant elm to restore floodplains impacted by emerald ash borer, in: Proceedings of the 4th International Workshop on Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, Res. Paper. PSW-GTR-240, pp. 317–323.
Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.

http://dx/doi.org/ 10.2307/1942040.
Koch, J.L., Carey, D.W., Knight, K.S., Poland, T.M., Herms, D.A., Mason, M.E., 2012. Breeding strategies for the development of emerald ash borer-resistant North American ash, in: Proceedings of the 4th International Workshop on the Genetics of Host–Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, Gen. Tech. Rep. PSW-GTR-240, pp. 235–239.
Kozlowski, T.T., 1997. Responses of woody plants to flooding and salinity. Tree Physiol. 17, 490. http://dx/doi.org/10.1093/treephys/17.7.490.
Krajecek, J.E., Williams, R.D., 1990. *Celtis occidentalis* L.: Hackberry, in: Burns, R.M., Honkala, B.H., tech. coord. (Eds.), Silvics of North America: Volume 2 Hardwoods, Agricultural Handbook 654. USDA Forest Service, Washington, D.C., p. 877.
Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika 29, 1–27.
Landhäusser, S.M., Lieffers, V.J., Silins, U., 2003. Utilizing pioneer species as a hydrological nurse crop to lower water table for reforestation of poorly drained boreal sites. Ann. For. Sci. 60, 741–748. http://dx/doi.org/10.1051/forest:2003068.
Landis, T.D., Dumroese, R.K., Haase, D.L., 2010. The Container Nursery Manual, Volume Seven: Seedling Processing, Storage and Outplanting. USDA Forest Service, Agricultural Handbook 674, Washington D.C.
Landscape Change Research Group, 2014. Change Tree Atlas (A Spatial Database of 134 Tree Species of the Eastern USA). USDA For. Serv. North. Res. Stn. http://www.nrs.fs.fed.us/ atlas/tree (accessed 3.3.15).
Larocque, G.R., 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. For. Sci. 48, 24–34.
Larsson, L.A., 2014. CooRecorder and Cdendro programs of the CooRecorder/Cdendro package. Cybis Elektronik.
Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556. http://dx/doi.org/10.1046/j.1365-2435.2002.00664.x.
Lenhart, C., Brooks, K., Davidson, M., Slesak, R., D'Amato, A., 2012. Hydrolic source characterization of black ash wetlands: Implications for EAB response. Presented at the AWRA Summer Specialty Conference on Riparian Ecosystems, Denver, CO, June 27-29.
Lenth, R.V., 2016. Least-Squares Means: The R Package lsmeans. J. Stat. Softw. 69, 1–33. http://dx/doi.org/10.18637/jss.v069.i01.
Lichvar, R.W., Banks, D.L., Kirchner, W.N., Melvin, N.C., 2016. The national wetland plant list: 2016 wetland ratings. Phytoneuron 30, 1–15. http://dx/doi.org/10.1016/ j.foreco.2016.05.050.
Lieffers, V.J., Macdonald, S.E., Hogg, E.H., 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23, 2070–2077. http://dx/doi.org/10.1139/x93-258.

Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., Branter, K., 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. 72, 286–292. http://dx/doi.org/10.5558/tfc72286-3.

Looney, Christopher E., D'Amato, A.W., Fraver, S., Palik, B.J., Reinikainen, M.R., 2016. Examining the influences of tree-to-tree competition and climate on size-growth relationships in hydric, multi-aged *Fraxinus nigra* stands. For. Ecol. Manag. 375, 238–248. http://dx/doi.org/10.1016/j.foreco.2016.05.050.

Looney, Christopher Edward, DAmato, A.W., Palik, B.J., Slesak, R., 2016. Canopy treatment influences growth of replacement tree species in *Fraxinus nigra* forests threatened by emerald ash borer in Minnesota, USA. Can. J. For. Res. http://dx/doi.org/10.1139/cjfr-2016-0369.

Looney, C.E., D'Amato, A.W., Palik, B.J., Slesak, R.A., 2015. Overstory treatment and planting season affect survival of replacement tree species in emerald ash borer threatened *Fraxinus nigra* forests in Minnesota, USA. Can. J. For. Res. 45, 1728–1738. http://dx/doi.org/ 10.1139/cjfr-2015-0129.

Lorimer, C.G., 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manag. 6, 343–360. http://dx/doi.org/10.1016/0378-1127(83)90042-7.

McCune, B., Grace, J.B., Urban, D.L., 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

McCune, B., Medford, M., 2011. PC-ORD Version 6: Multivariate analysis of ecological data. MjM Software Design, Glendon Beach, OR.

McDonald, P.M., Abbott, C.S., 1994. Seedfall, regeneration, and seedling development in group-selection openings. USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Megonigal, J.P., Conner, W.H., Kroeger, S., Sharitz, R.R., 1997. Aboveground production in southeastern floodplain forests: a test of the subsidy–stress hypothesis. Ecology 78, 370–384. http://dx/doi.org/10.1890/0012-9658(1997)078 [0370:APISFF] 2.0.CO;2.

Meko, D.M., Touchan, R., Anchukaitis, K.J., 2011. Seascorr: A MATLAB program for identifying the seasonal climate signal in an annual tree-ring time series. Comput. Geosci. 37, 1234–1241. http://dx/doi.org/10.1016/j.cageo.2011.01.013.

Minnesota Wildflowers, 2016. https://www.minnesotawildflowers.info (accessed 8.22.16).

MNDNR, 2003. Field guide to the native plant communities of Minnesota: The Laurentian mixed forest province. Minnesota Department of Natural Resources, St. Paul, MN.

Morin, X., Augspurger, C., Chuine, I., 2007. Process-based modeling of species' distributions: What limits temperate tree species' range boundaries? Ecology 88, 2280–2291. http://dx/doi.org/10.1890/06-1591.1. PMID:17918406.

National Climate Data Center, 2015. Minnesota Climate Division 2. http://www.ncdc.noaa.gov/ temp-and-precip/drought/historical-palmers/ (accessed 5.28.15).

National Oceanic and Atmospheric Administration, 2015. National Climatic Data Center: Minnesota Climate Division 2. http://www1.ncdc.noaa.gov/pub/data/cirs/ (accessed 7.10.15).
Native Plant Information Network, 2016. Lady Bird Johns. Wildflower Cent. https://www.wildflower.org/explore/ (accessed 8.22.16).
Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76, 521–547. http://dx/doi.org/ 10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2
Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. Front. Ecol. Environ. 3, 421–428. http://dx/doi.org/10.1890/1540-9295(2005)003[0421:UVAAFE]2.0.CO;2.
Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics: Updated Edition. John Wiley & Sons, Inc., New York, NY.
Orwig, D., 2002. Ecosystem to regional impacts of introduced pests and pathogens: Historical context, questions and issues. J. Biogeogr. 29, 1471–1474. http://dx/doi.org/10.1046/j.1365-2699.2002.00787.x.
Palik, B.J., Kastendick, D., 2010. Response of seasonal pond plant communities to upland forest harvest in northern Minnesota forests, USA. For. Ecol. Manag. 260, 628–637. http://dx/doi.org/10.1016/j.foreco.2010.05.019.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2012. Tree regeneration in black ash (*Fraxinus nigra*) stands exhibiting crown dieback in Minnesota. For. Ecol. Manag. 269, 26–30. http://dx/doi.org/10.1016/j.foreco.2011.12.020.
Palik, B.J., Ostry, M.E., Venette, R.C., Abdela, E., 2011. *Fraxinus nigra* (black ash) dieback in Minnesota: Regional variation and potential contributing factors. For. Ecol. Manag. 261, 128–135. http://dx/doi.org/10.1016/j.foreco. 2010.09.041.
Palik, B.J., Streblow, D., Egeland, L., Buech, R., 2007. Landscape variation of seasonal pool plant communities in forests of northern Minnesota, USA. Wetlands 27, 12–23. http://dx/doi.org/10.1672/0277-5212(2007)27[12:LVOSPP]2.0.CO;2.
Peck, J., 2010. Multivariate anaylysis for community ecologists: step-by-step using PC-ORD. MjM Software Design, Gleneden Beach, OR.
Pedlar, J.H., McKenney, D.W., Aubin, I., Beardmore, T., Beaulieu, J., Iverson, L., O'Neill, G.A., Winder, R.S., Ste-Marie, C., 2012. Placing forestry in the assisted migration debate. BioScience 62, 835–842. http://dx/doi.org/10.1525/ bio.2012.62.9.10
Percival, D.B., Constantine, W.L.B., 2006. Exact simulation of Gaussian time series from nonparametric spectral estimates with application to bootstrapping. Stat. Comput. 16, 25–35. Gleneden Beach, OR. http://dx.doi.org/10.1007/s11222-006-5198-0.
Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., 2016. nlme: Linear and nonlinear mixed effects models. https://CRAN.R-project.org/package=nlme (accessed 3.5.16).
Poland, T.M., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. J. For. 104, 118–124.
Preisser, E.L., Oten, K.L.F., Hain, F.P., 2014. Hemlock woolly adelgid in the eastern United States: What have we learned? Southeast. Nat. 12, 1–15. http://dx/doi.org/

10.1656/ 058.013.s604.
Pretzsch, H., 2005. Diversity and productivity in forests: evidence from long-term experimental plots, in: Forest Diversity and Function, Ecological Studies. Springer: Verlag, Berlin-Heidelberg, pp. 41–64.
PRISM Climate Group, 2015. PRISM climate data. Northwest Alliance Comput. Sci. Eng. http://www.prism.oregonstate.edu/recent/ (accessed 1.11.15).
Pryor, S.C., Scavia, D., Downer, C., Gaden, M., Iverson, L.R., Nordstrom, R., Patz, J., Robertson, G.P., 2014. Midwest, in: Melillo, J.., Richmond, T.C., Yohe, G.W. (Eds.), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, Washington, D.C., pp. 418–440.
Pugh, S.A., Liebhold, A.M., Morin, R.S., 2011. Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can. J. For. Res. 41, 2165–2175. http://dx/doi.org/10.1139/x11-138.
Qian, H., Yuan, X.-Y., Chou, Y.-L., 2003. Forest vegetation of northeast China, in: Kolbeck, J., Srutek, M., Box, E.O., eds., Forest Vegetation of Northeast Asia. Springer, Dordrecht, The Netherlands, pp. 181–230.
Quantum GIS Development Team, 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project.
R Core Team, 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rebertus, A.J., Burns, B.R., Veblen, T.T., 1991. Stand dynamics of *Pinus flexilis*-dominated subalpine forests in the Colorado Front Range. J. Veg. Sci. 2, 445–458. http://dx/doi.org/ 10.2307/3236026.
Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Can. J. Bot. 82, 1273–1283. http://dx/doi.org/ 10.1139/b04-091.
Rogers, D.A., Rooney, T.P., Olson, D., Waller, D.M., 2008. Shifts in southern Wisconsin forest canopy and understory richness, composition, and heterogeneity. Ecology 89, 2482–2492. http://dx/doi.org/ 10.1890/07-1129.1.
Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. For. Ecol. Manag., Forest Dynamics and Ungulate Herbivory : From Leaf to Landscape 181, 165–176. http://dx/doi.org/ 10.1016/S0378-1127(03)00130-0.
Rouvinen, S., Kuuluvainen, T., 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27, 890–902. http://dx/doi.org/ 10.1139/cjfr-27-6-890.
Roy, V., Ruel, J.-C., Plamondon, A.P., 2000. Establishment, growth and survival of natural regeneration after clearcutting and drainage on forested wetlands. For. Ecol. Manag. 129, 253–267. http://dx/doi.org/ 10.1016/S0378-1127(99)00170-X.
Royo, A.A., Carson, W.P., 2006. On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. 36, 1345–1362. http://dx/doi.org/ 10.1139/x06-025.
Schwinning, S., Weiner, J., 1998. Mechanisms determining the degree of size asymmetry

in competition among plants. Oecologia 113, 447–455. http://dx/doi.org/ 10.1007/ s004420050397.
Scott, G.A.J., 1995. Canada's Vegetation: A World Perspective. McGill-Queen's Press, Montreal, Quebec.
Shields, J.M., Webster, C.R., 2007. Ground-layer response to group selection with legacy-tree retention in a managed northern hardwood forest. Can. J. For. Res. 37, 1797–1807. http://dx/doi.org/ 10.1139/X07-052.
Shipley, B., 1999. Testing causal explanations in organismal biology: Causation, correlation and structural equation modelling. Oikos 86, 374–382. http://dx/doi.org/ 10.2307/3546455.
Shipley, B., Keddy, P.A., Moore, D.R.J., Lemky, K., 1989. Regeneration and establishment strategies of emergent macrophytes. J. Ecol. 77, 1093–1110. http://dx/doi.org/ 10.2307/2260825.
Slavicek, J.M., Knight, K.S., 2012. Generation of American elm trees with tolerance to Dutch elm disease through controlled crosses and selection., in: Sniezko, R.A., Yanchuk, A.D., Kliejunas, J.T., Palmieri, K.M., Alexander, J.M., Frankel, S.J. (Eds.), Proceedings of the Fourth International Workshop on the Genetics of Host-Parasite Interactions in Forestry: Disease and Insect Resistance in Forest Trees. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, Gen. Tech. Rep. PSW-GTR-240pp. 342–346.
Slesak, R.A., Lenhart, C.F., Brooks, K.N., D'Amato, A.W., Palik, B.J., 2014. Water table response to harvesting and simulated emerald ash borer mortality in black ash wetlands in Minnesota, USA. Can. J. For. Res. 44, 961–968. http://dx/doi.org/10.1139/cjfr-2014-0111.
Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1996. The Practice of Silviculture: Applied Forest Ecology, 9th ed. John Wiley and Sons, New York, NY.
Snyder, S.A., 1992. *Quercus bicolor*. Fire Eff. Inf. Syst. http://www.fs.fed.us/database/feis/ (accessed 5.28.15).
Speer, J.H., 2010. Fundamentals of Tree-ring Research. University of Arizona Press, Phoenix, AZ.
Stampfli, A., Zeiter, M., 2004. Plant regeneration directs changes in grassland composition after extreme drought: a 13-year study in southern Switzerland. J. Ecol. 92, 568–576. http://dx/doi.org/ 10.1111/j.0022-0477.2004.00900.x.
StataCorp, 2011. Stata, Stata Statistical Software: Release 12. StataCorp LP., College Station, TX.
Taborton, D., 2015a. Terrain Analysis using Digital Elevation Models (TauDEM Version 5). Utah State Univ. Hydrol. Res. Group. http://hydrology.usu.edu/taudem/taudem5/ index.html (accessed 12.9.16).
Takyi, S.K., Hillman, G.R., 2000. Growth of coniferous seedlings on a drained and mounded peatland in central Alberta. North. J. Appl. For. 17, 71–79.
Tardif, J., Bergeron, Y., 1999. Population dynamics of *Fraxinus nigra* in response to flood-level variations, in northwestern Quebec. Ecol. Monogr. 69, 107–125. http://dx/doi.org/10.1890/0012-9615(1999)069[0107:PDOFNI]2.0.CO;2.

Tardif, J., Bergeron, Y., 1997. Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. Can. J. For. Res. 27, 108–116. http://dx/doi.org/10.1139/x96-150.
Tardif, J., Bergeron, Y., 1993. Radial growth of *Fraxinus nigra* in a Canadian boreal floodplain in response to climatic and hydrological fluctuations. J. Veg. Sci. 4, 751–758. http://dx/doi.org/10.2307/3235611.
Tardif, J.C., Conciatori, F., 2006. Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, southwestern Quebec, Canada. Can. J. For. Res. 36, 2317–2330. http://dx/doi.org/10.1139/x06-133.
Tardif, J.C., Stevenson, D., 2001. Radial growth-climate association of *Thuja occidentalis* L. at the northweastern limit of its distribution, Manitoba, Canada. Dendrochronologia 19, 1–9.
Telander, A.C., Slesak, R.A., D'Amato, A.W., Palik, B.J., Brooks, K.N., Lenhart, C.F., 2015. Sap flow of black ash in wetland forests of northern Minnesota, USA: Hydrologic implications of tree mortality due to emerald ash borer. Agric. For. Meteorol. 206, 4–11. http://dx/doi.org/10.1016/j.agrformet.2015.02.019.
The PLANTS database, 2016. . USDA Nat. Resour. Conserv. Serv. http://plants.usda.gov (accessed 8.22.16).
Tilman, D., 1982. Resource competition and community structure. Monogr. Popul. Biol. 17, 1–296.
Townsend, A.M., Bentz, S.E., Douglass, L.W., 2005. Evaluation of 19 American elm clones for tolerance to Dutch elm disease. J. Environ. Hortic. 23, 21–24.
Tredici, P.D., 2001. Sprouting in temperate trees: A morphological and ecological review. Bot. Rev. 67, 121–140. http://dx/doi.org/10.1007/BF02858075.
University of Minnesota Extension and MNDNR, 2011. Ash Management Guidelines for Private Forest Landowners. University of Minnesota Extension Service, St. Paul. MN.
U.S. Geological Survey, 2016. The National Map: 3D Elevation Program (3DEP). http://nationalmap.gov/3DEP/3dep_prodserv.html (accessed 12.30.16).
USDA NRCS, 2016. Web Soil Survey. http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/soils/home/?cid=nrcs142p2_053587 (accessed 12.30.16).
Walsh, J.D., Wuebbles, D., Hayhoe, K., Kossin, J., Kunkel, K., Stephens, G., Thorne, P., Vose, R.P., Wehner, M., Willis, J., 2014. Chapter 2: Our Changing Climate, in: Melillo, J.., Richmond, T.C., Yohe, G.W. (Eds.), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Change Research Program, pp. 19–67.
Wang, J., Wu, L., Zhao, X., Fan, J., Zhang, C., Von Gadow, K., 2013. Influence of ground flora on *Fraxinus mandshurica* seedling growth on abandoned land and beneath forest canopy. Eur. J. For. Res. 132, 313–324. http://dx/doi.org/10.1007/s10342-012-0676-8.
Waring, K.M., O'Hara, K.L., 2005. Silvicultural strategies in forest ecosystems affected by introduced pests. For. Ecol. Manag. 209, 27–41. http://dx/doi.org/10.1016/

j.foreco.2005.01.008.
Weiner, J., 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5, 360–364.
Whitehill, J.G.A., Herms, D.A., Bonello, P., 2010. Exploring the molecular and biochemical basis of ash resistance to emerald ash borer, in: Proceedings of the Symposium on Ash in North America. USDA Forest Service, Northern Research Station, Newton Square, PA, Gen. Tech. Rep. NRS-P-72, pp. 9–23.
Williams, M.I., Dumroese, R.K., 2013. Preparing for climate change: forestry and assisted migration. J. For. 111, 287–297. http://dx/doi.org/10.5849/jof.13-016.
Wilson, E.R., Vitols, K.C., Park, A., 2007. Root characteristics and growth potential of container and bare-root seedlings of red oak (*Quercus rubra*). New For. 34, 163–176. http://dx/doi.org/10.1007/s11056-007-9046-7.
Wilson, S.D., 1991. Variation in competition in eucalypt forests: The importance of standardization in pattern analysis. J. Veg. Sci. 2, 577–586. doi:10.2307/3236169
Youngblood, A., Titus, B., 1996. Clearcutting - a regeneration method in the boreal forest. For. Chron. 72, 31–36. http://dx/doi.org/10.5558/tfc72031-1.
Yulianti, J.S., Burn, D.H., 1998. Investigating links between climatic warming and low streamflow in the Prairies region of Canada. Can. Water Resour. J. Rev. Can. Ressour. Hydr. 23, 45–60. http://dx/doi.org/10.4296/cwrj2301045.
Zang, C., Biondi, F., 2015. treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography 38, 431–436. http://dx/doi.org/10.1111/ecog.01335.
Zasada, J.C., Viereck, L.A., Foote, M.J., Parkenson, R.H., Wolff, J.O., Lankford Jr., L.A., 1981. Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. For. Chron. 57, 57–65. http://dx/doi.org/10.5558/tfc57057-2.